Proceedings of the
13th International Marine Biological Workshop
The Marine Fauna and Flora of Moreton Bay, Queensland

Volume 1

Edited by Peter J.F. Davie and Julie A. Phillips

Proceedings of the Thirteenth International Marine Biological Workshop

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Cover Picture: view south across Pumicestone Passage, northern Moreton Bay, towards the Glasshouse Mountains. Insets: a cluster of Blue Periwinkles (*Austrolittorina unifasciata*); and Dr Xinzheng Li of the Chinese Academy of Sciences, Qingdao, China, looking for shrimps in a tidal pool during the Moreton Bay Workshop.

NOTE

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PREFACE

The Thirteenth International Marine Biological Workshop on the Fauna and Flora of Moreton Bay, Queensland, was held from the 7th-25th February 2005 at the Moreton Bay Research Station, Dunwich, North Stradbroke Island. The Workshop was organised by the Southeast Queensland Branch, Australian Marine Sciences Association, and in particular Peter Davie, Julie Phillips, Ian Brown, Mara Wolkenhauer, Ian Tibbetts and Nerida Wilson. Much needed sponsorship was provided by the Queensland Government (Queensland Museum; Department of Primary Industries and Fisheries; Department of Natural Resources and Water), the University of Queensland (Faculty of Biological and Chemical Sciences, Centre for Microscopy and Microanalysis, Centre for Marine Studies), the Port of Brisbane, Brisbane City Council and Consolidated Rutile Limited. This is the first workshop where such a large group of experienced marine scientists have simultaneously collaborated on research projects to generate new data on the species and ecology of Moreton Bay. For 18 days, nearly 40 marine biologists from the United Kingdom, Germany, Singapore, Taiwan, United States of America, New Zealand and Australia worked together to collect field data. This involved intertidal hand collecting, snorkelling and SCUBA diving, and dredging and grab-sampling using the DPI&F Research Vessel, the *Tom Marshall*. Collections were analysed and sorted in the laboratory, and data and specimens were subsequently further worked on at home institutions. The result of this research is the three volume Proceedings amounting to nearly 900 pages (the present 2008 volume to be followed by two more in early 2009).

The Moreton Bay Workshop followed in the footsteps of marine biological workshops in Western Australia (Albany, 1988; Rottnest Island, 1991, 1996; Houtman Abrolhos Islands, 1994; Dampier, 2000; Esperance, 2002), and the Northern Territory (Darwin, 1993). All have been part of an international series initiated by Prof. Brian Morton at the University of Hong Kong, with other successful workshops having been held in Hong Kong, the Portuguese Azores and California. It was established to allow international and interstate scientists the opportunity to work with local scientists to generate new scientific information about this important southeast Queensland marine environment. As well, it was a marvellous opportunity for students to meet and work with leading scientists from many fields of marine research. Each scientist paid their own transport costs to Brisbane, and a participation fee that went towards basic accommodation and living expenses. The money raised from sponsorship met all additional expenses including boat and equipment hire, SCUBA diving costs and chemicals, tubes, bottles, and other expendables.

These workshops have proven to be a very successful model for generating an extraordinary amount of new data in a very short space of time, and as they are subsidised by the scientists themselves, are extremely cost effective. It is to be hoped that more such workshops can be organised at other localities along the Queensland coast in the years to come, and they will garner the full financial support from government and industry that they deserve.

Peter J.F. Davie & Julie A. Phillips

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ACKNOWLEDGEMENTS

WELCOME TO COUNTRY

Gurring and anami Biami Inta, which means welcome to this land and may God bless us all.

Long before the Europeans came, our Aboriginal people lived on this Island and travelled to the many areas of this island and the other Bay Islands gathering and hunting. Myora was a large camping ground and there were three tribes that we know of, Ngughi from Moreton Island, Nuntikel from Stradbroke Island, and Geonpul were from as far south as the Tweed.

The middens that are to be found from one end of the Island to the other, range in age from 3000 years to 22,000 years old as recorded by archaeologists.

Aboriginal people have instincts close to nature, in observing every detail. People with this gift, see things with seeing eyes, and love nature very very much — more than those, who look and see nothing. For instance, when parrots are seen in extra large numbers, it is a sign of a good mullet season. An abundance of honey is indicated when when the tea trees are in full bloom. Long lines of hairy caterpillars travelling, are a sign of fish travelling up the coast to their spawning grounds. If a certain wind blows, the spore from the Elk Horn will be propagated.

An old Aboriginal friend Will McKenzie told many tales of animals, birds, marine life and reptiles. Some were spiritual, others were demonstrated in a corroborree which had every child in his midst enthralled with his storytelling.

The Bay was a source of beautiful shellfish, dugong, turtle, crustaceans, and fish in abundance. On the land there was bush tucker for the taking. Our culture is rich, and I pride myself that I knew two Grannies who were the last of the tribes, and who gave me their knowledge. As a young girl we would be taken onto the banks and taught about the poisonous cone shell. Also, the bailer shell — we had to let the small ones grow to a very large size, so they could be used as water containers. The quampi, Aboriginal word for Pearl shell, were gathered for their food value, and for their beautiful pearls found in the shell. They were used for bartering with Europeans for flour and tobacco. From the inner bark of the cotton tree they made string which was made into fishing nets, and dugong nets, and fishing lines. Stones for knives and axes were traded from the mainland. Stones axes and spears heads were bound with string and then made very secure with resin made from the grass tree.

The dugong was a good source of food for our people. Oil was extracted and used for medicinal purposes, internally and externally. Honey was an important source of food and was used for healing of cuts and sores. We now know that hospitals are calling it medicated honey for ulcers. The medicinal plant cunjevoi was used for stings and burns.

In 1891 Aboriginal people were then put on to the mission, and of course they had to be under the jurisdiction of a Superintendent. Our language was stopped. We were not allowed to use the language. We were prohibited from using it under threat of being removed to a mainland reserve. Today we are trying to revive it.

We the Minjerribah Moorgumpin Elders work very hard for our Community and have always looked towards a better future for our young people. We have very good relationships with the staff and principle of our Secondary and Primary School, and State and Federal Governments on all levels. We have a MoU with Redland Shire Council. We are working with our local police towards having camps for non-indigenous and indigenous students. We are also involved in a fire prevention project with our Fire Department and students.

My cultural talks keep me very busy. Last year I presented talks to two thousand students. I am involved with all organisations on the Island, environmental and health programmes, and have a good understanding with the two mining companies.

I can say I have been involved in two books, which provide revenue for the Elders. I am proud of my achievements as my education only went to grade six. I did a six month managerial course at

the age of seventy for which I am very proud My husband Pat worked for the mines for 34 years. We had 5 children in 4 years, including twins, 15 grandchildren, 12 great-grandchildren and another on the way.

Our learned visitors ... we as a whole must work together to preserve what we all have, to keep our waterways and oceans a healthy preserve. Our fish stocks and everything in our environment must be preserved and treasured.

We the Aboriginal people watched what we did on the sea and the land — don't take too much of any one thing and always keep it in balance.

The history of our shared experiences brings together two different timelines, two different cultures and two different laws. All Australians can share in the pride and knowledge that this country is home to the oldest living culture in the world.

To our lovely visitors, please enjoy our Island, it's hospitality and scenic views. Each, of us, is unique in our own special way, not forgetting, where we are from, and never losing sight of where we are going.

Thank you and God bless you all.

Aunty Margaret Iselin

President
Minjerribah Moorgumpin
Elders-in-Council
Aboriginal Corporation
08.02.05

INTRODUCTION

The Marine Fauna and Flora of Moreton Bay Workshop: a focus on species

Peter J.F. Davie & Julie A. Phillips

Moreton Bay, in southeast Queensland, is one of Australia's most outstanding natural areas. It is a place of great beauty and variety on the edge of one of Australia's largest cities. However, the southeast Queensland region is one of the fastest growing large urban areas in the developed world, and this inevitably exerts enormous pressure on Moreton Bay. A healthy marine ecosystem is crucial for maintaining the important commercial fisheries, and also for the enormous numbers of recreational users that pour out of Brisbane and nearby centres to enjoy this unique environment.

Of great interest to scientists is the fact that Moreton Bay lies at the heart of a major biogeographic overlap zone. It is here that the southern and northern biotas meet, forming unusual communities of both temperate and tropical species. This is enhanced by the unique geography of Moreton Bay, that has allowed the development of a diversity of habitats all in close proximity, including mud and sand flats, seagrass, mangrove and macroalgal-dominated intertidal areas, extensive soft-bottom subtidal communities, rocky shores, reefs covered in coral, and pristine sandy ocean beaches. Furthermore, the sandy oceanic-influenced eastern bay differs markedly from the muddy estuarine western Bay, and this contributes to the diversity of habitats, and the development of a remarkably diverse fauna and flora. This may help explain why there appears to be a relatively large number of apparently indigenous species — prior to the 2005 workshop there were about 27 species known only from Moreton Bay (Davie & Hooper 1998). With the many new species described as a result of the Workshop, the number of indigenous species may prove to be considerably more.

While it remains a remarkably beautiful system, it is clear that quality care and management will be essential if it is to survive in a healthy state for future generations. The impor-

tance of Moreton Bay and the Brisbane River to the people of southeast Queensland is clearly illustrated by the establishment of the *Moreton Bay Marine Park* in 1993, with a revised and improved management zoning plan released this year. Another major initiative has been the commitment and financial support given to the Healthy Waterways program of the Moreton Bay Waterways and Catchments Partnership, a whole-of-government and community collaboration that has produced some very significant results, especially in understanding nutrient cycling and the impact of sewage on the western Bay. The 1999 book *Moreton Bay Study: A Scientific Basis for the Healthy Waterways Campaign* (Dennison & Abal 1999), for the first time laid down an important foundation for understanding the ecological dynamics of the Bay and the Brisbane River.

Nevertheless Moreton Bay's biodiversity remains relatively poorly known. Clearly much more effort to discover and document the species-level diversity of Moreton Bay is urgently required to answer many important questions. Are there more new species endemic to Moreton Bay, and do such species need special management considerations? Are there local marine species that may have bioactive compounds important for medical research? What specific organisms may be crucial to the feeding ecology of the endangered dugong and green turtle? What is the ecology of some common species of algae, and what causes some algal and cyanobacterial species to form dramatic seasonal blooms? Such questions were the impetus to convene the 2005 workshop, and never before has such a diverse group of specialists been convened at the same time and place to investigate them.

A HISTORY OF STUDY

It was the emergence of marine biology and ecology as scientific disciplines during the 1950s

FIG. 1. Landsat image of Moreton Bay. © copyright Commonwealth of Australia (Geoscience Australia) [2008].

that ignited a growing emphasis on marine studies in Moreton Bay. Since then the Bay has received much scrutiny, and, especially since the 1970s, it has been the focus of a number of scientific symposia which have covered diverse topics ranging from geology to terrestrial and marine plant and animal communities, to environmental management. In particular these have included:

• *Stradbroke Island Symposium*, Point Lookout, North Stradbroke I., 15–17 June, 1974, Royal Society of Queensland and ANZAAS – Qld Division (see Stevens & Monroe 1975)

• *Northern Moreton Bay Symposium*, 1978, Royal Society of Queensland (Bailey & Stevens 1979).

• *Focus on Stradbroke*, Point Lookout, North Stradbroke I., 11–12 Aug., 1984, Royal Society of Qld (see Coleman, Covacevich & Davie 1984).

• *The Brisbane River – its Future and Management*, 20 Aug., 1988, Australian Littoral Society (see Davie, Stock & Low Choy 1990).

• *Moreton Bay in the Balance*, Brisbane, 14 July, 1989, Australian Marine Science Consortium & Australian Littoral Society (see Crimp 1992).

• *Future Marine Science in Moreton Bay*, Feb., 1993, School of Marine Science, University of Qld (see Greenwood & Hall, 1993).

• *Moreton Bay and Catchment Conference*, Dec. 1996, School of Marine Science, University of Qld (see Tibbets, Hall & Dennison 1998).

These symposia and their subsequent publications have all been vital and timely tools to draw together the gradually evolving research data on Moreton Bay, and have been used extensively for devising strategies for environmental management and conservation planning in the region. The 2005 Moreton Bay Workshop differed from these earlier efforts by gathering a team of scientists together not to summarise existing data, but to actively generate new information in a short but intense period of study and research.

A REMARKABLE BIODIVERSITY

A major result of the Workshop was a significant contribution of new knowledge on the marine species of Moreton Bay. Over the last two decades much of the scientific focus has been related to water quality monitoring, and while this has had important management implications in terms of trying to achieve an overall healthy ecosystem, such studies need to be underpinned by more comprehensive taxonomic inventories and data on species biology. Ecosystems are complex, and few, if any, resources are being currently directed towards biological monitoring of species presence and abundance. Such monitoring can give a much more accurate assessment of system health, than simply measuring a limited number of physico-chemical parameters during a narrow sampling window. Furthermore, if we are to identify invasions of marine pests, protect rare and threatened species, identify biodiversity hotspots, and predict the impacts of climate change, then we need to have strong baseline data on taxonomic biodiversity and individual species biology. Such information is also crucial for effective marine park zoning.

Taxonomy is the foundation for not only all biological scientific study, but also for environmental management and conservation initiatives. It is not possible to deal with a species that is not defined by a name because it cannot be placed in national or international contexts in terms of its 'uniqueness' or 'commonality', and it cannot even be individually discussed without that all important name-tag that allows it to exist in our language and consciousness. Similarly, science based on inaccurate species names (misidentifications) can be meaningless. Different but related species can have markedly different physiological, ecological and reproductive characteristics that must be individually taken into account.

The urgent need for taxonomic studies is clearly illustrated by the numerous taxonomic papers resulting from this Workshop. These studies report on the discovery of a remarkable total of 53 new species, six new genera, and even a new family. In addition, over 80 new distributional records are provided for previously described species, with many of these new to not only the Moreton Bay region, but also to Queensland and Australia. This increase in known biodiversity is even more extraordinary when you consider the narrow interval of sampling of little more than two weeks, and the relatively small sampling area mostly con-

fined to the central-eastern part of the Bay. A simple extrapolation of this result clearly indicates that there are potentially hundreds more new species to be discovered right here in the shallow waters so close to Brisbane — especially if a wider group of experts could be marshalled together, and a longer period for collections was available. It is well established in the scientific literature that species richness is inextricably correlated with sampling effort and the size of the area sampled, and that marine communities are dynamic entities that are both spatially and temporally variable.

The present volume of the Proceedings will be subsequently accompanied by publication of another two volumes, one being a complete taxonomic revision of the hard coral species living inside the Bay, their fossil record in the Bay, and their distributions in southeastern Australia. This work also reviews and updates records from the broader Moreton Bay region, and reviews the history of corals in Moreton Bay based on Queensland Museum collections from 1924 to the present. Such a work is, of course, not just the result of the 2005 Workshop, but the authors used the workshop as an opportunity to finish investigating and mapping many new areas. Of a total of 68 coral species now known to live in the inside waters of Moreton Bay, 22 species are reported for the first time. Such basic work as this, is crucial to fully understand the changing dynamics of coral communities, and to understand what might be the ecological response to global climate change, rising sea levels, and rising sea temperatures.

Changes in species distributions as temperate species retreat and more tropical species expand their ranges, is one of the most accurate and sensitive indicators of the impact of climate change. We are fortunate to now have such reliable data for scleractinian corals, but for most other groups such knowledge is still critically lacking. Because of the lack of detailed baseline data, it is not possible to be sure whether the recent record of the seagrass *Halophila minor* in Moreton Bay (Phillips *et al.*, this volume) represents a latitudinal shift in the distribution of this formerly strictly tropical species, or is due to it having been previously confused with

the highly variable *Halophila ovalis*, and simply overlooked. Moreton Bay, being placed as it is on the cusp between the temperate and tropical bioregions of eastern Australia, makes it the ideal place for biological monitoring of climate change, but this hinges very much on good baseline data.

The workshop also served as a springboard to compile the first-ever regional lists of some major faunal groups such as jellyfish, hydroids, corals, molluscs, shrimps, parasitic isopods, tunicates and fish. These species lists will be necessary and invaluable aids for all researchers, students, environmental managers, and conservation planners, in identifying species and assessing biodiversity levels around the Bay, both now and into the future. As an indication of the scale of biodiversity that is now being documented, the broader Moreton Bay Marine Park area now has 1154 species of fish, 944 gastropod molluscs, 351 bivalve molluscs and 95 species of the Ascidiacea. However many groups still lack this basic level of documentation, and the compilation and provision of more such lists should be seen as a priority.

Although taxonomy was an important part of the workshop, there were many other research projects undertaken. These were wide ranging in scope, and included work on animal behaviour, algal and animal physiology, biotic surveys, ecology, and environmental impacts.

Environmental management, conservation strategies, and marine park planning, must all be underpinned by science and informed by ongoing research. We need to know the current status of species and communities in order to effectively manage and protect marine habitats now and into the future. Also the effectiveness of our conservation management efforts must be measurable, and have ongoing assessment through monitoring and feedback systems.

THE FUTURE

The Healthy Waterways work reported in Dennison & Abal (1999) was a well-funded thorough study of water quality, nutrient levels, and physical processes, however it did not in itself answer many of the other important questions regarding the maintenance of diverse,

healthy, and sustainable ecological communities. Indeed it was freely admitted that there is a diverse biota 'of economic and ecological importance' that was beyond the scope of that study. Moreton Bay urgently needs further major Bay-wide studies by diverse groups of scientists to systematically map this biota and describe the ecological inter-relationships.

Moreton Bay is still a poor cousin when compared to the study and resources that have been poured into gaining an ecological understanding of Port Phillip Bay, adjacent to Melbourne. From 1947 to 1952 CSIRO conducted a monthly sampling of Port Phillip Bay waters at six stations from Hobsons Bay to Bass Strait. This was followed by a six-year survey (1957–1963) by the National Museum of Victoria and the Victorian Fisheries and Wildlife Department, that involved comprehensive collections made by SCUBA diving and epibenthic sledge in each of 70 grid squares across the entire bay, disclosing for the first time the great richness and diversity of the Bay ecosystem. From 1968–1975 there were a number of quantitative biological surveys undertaken to provide a baseline with which to assess long term affects of urbanisation on the Bay. This included work on macrobenthic species composition and abundance data (Poore & Rainer 1974; Poore *et al*. 1975), and biomass data collected from three stations during 1973–1975 (Poore & Rainer, 1979; Poore 1993). Finally from 1992 to 1996 there was the intensive multi-disciplinary $12 million Port Phillip Bay Environmental Study (Harris *et al*. 1996). Those studies are international benchmarks to which Queensland should also aspire for its own important Bay.

Biomass is a critical determinant of nutrient-cycling variables, yet reliable estimates of benthic faunal biomass are completely lacking for Moreton Bay. Wilson *et al*. (1993) estimated that, in Port Phillip Bay, suspension feeders (mostly bivalve molluscs) comprise half of the benthic macroinvertebrate biomass, and process a volume of water equivalent to the entire Bay in 16–17 days. Suspension feeders are estimated to be responsible for 15% of all organic matter ingested by benthic macroinvertebrates, but may account for over 40% of total assimi-

lation of organic material. Deposit feeders (mostly crustaceans, echinoids and polychaete worms) make up about 35% of total macro-benthic biomass, and in a single year, are estimated to process a volume of sediment equivalent to the top 13 mm of Port Phillip Bay sediments. Estimates of net annual secondary production from Port Phillip Bay by both benthic deposit- and suspension-feeding macro-invertebrates is about 62,700 tonnes C. By comparison, the productivity of benthic organisms has so far been virtually ignored in Moreton Bay, and yet, given the unique geography and rich subtropical sediments, their contribution to net productivity may well exceed the figures estimated for Port Phillip Bay. Direct measurements of secondary production by benthic invertebrates are needed to firmly establish the important role of these organisms in the ecology of Moreton Bay.

Benthic habitat mapping across Moreton Bay still needs a significant amount of attention. The work of Stevens & Connolly (2005) marked a quantum leap forward in mapping and classifying macrobenthic habitat types by using a compact video array at 78 sites spaced 5 km apart. In this way they were able to gather data for 2400 km² from estuarine shallow subtidal waters to offshore areas to the 50-m isobath. They recognised nine habitats, with only one being on hard substrate. These included previously unreported deep-water algal and soft coral reefs, and new areas of seagrasses. Nevertheless such a visual method is limited to some extent by water clarity, especially in the western part of the Bay; and at sites spaced 5 km apart, it is still a relatively course survey. Many of these zones would benefit by finer scale surveying and by ground-truthing using a variety of collecting techniques, as Stevens & Connolly themselves acknowledge.

Indeed, not all habitat types that appear similar have the same species composition. As Davie & Hooper (1998) reported, the sponge species composition at various hard bottom reefal sites both inside and outside the Bay can vary quite dramatically (Fig. 2). In general, there is less than a 20% overlap in species composition between adjacent communities; and this drops to no more than 6% when more
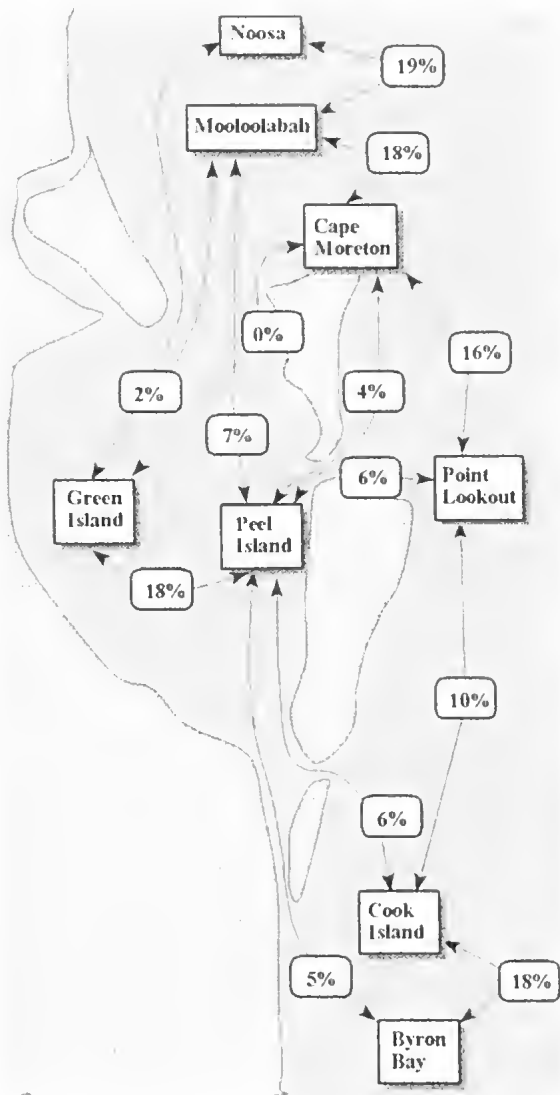
FIG. 2. A schematic representation showing percentage of sponge species shared between study sites within Moreton Bay, and those outside the Bay. After Davie & Hooper (1998).

distant sites inside and outside the Bay are compared. To reinforce this point, there is only 16% overlap in sponge species between Point Lookout and Cape Moreton which otherwise appear to be identical subtidal rocky reef habitats. This spatial heterogeneity has considerable implications for marine park planning which seeks to protect a representative sample of the biota. Similar-looking communities may be dramatically different in species composition

and thus needing separate conservation strategies.

The new Moreton Bay Marine Park Zoning Plan of 2008 has seen an increase in Green Zones to 16% of the marine Park area. This is to be applauded, as is the decision to undertake monitoring studies to assess, for the first time, the effectiveness of the new zones in protecting biodiversity. However, the zoning process has also starkly highlighted the lack of effective baseline data available on species level diversity, community structure, and the dynamics of communities in space and time.

Significant gaps continue to exist in our knowledge base of the marine biota of Moreton Bay. There are undoubtedly many new species yet to be discovered by science, and many species remain poorly known. Until we are able to begin to gather and interpret some long term datasets, as has been done for Port Phillip Bay, then we will continue to struggle in our attempts to ensure the health and productivity of Moreton Bay into the future.

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New species of Raspailiidae (Porifera: Demospongiae: Poecilosclerida) from southeast Queensland

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ABSTRACT

Extensive surveys of the marine benthos throughout tropical Australasia over the past two decades have revealed a large number of sponge species, most of which appear to be new to science. Even in the comparatively well-known Moreton Bay region, we discovered four new species belonging to three genera of the family Raspailiidae, and also increased the number of known species living in this area from three to eleven, in some cases greatly increasing their known distributional range. Other new extralimital records of these species are provided, as is a revised checklist of the Australian raspailiid fauna. ❑ *Porifera, Demospongiae, Poecilosclerida, Microcionina, Raspailiidae, Raspailia, Aulospongus, Ceratopsion, Sollasella, Echinodictyum, new species, taxonomy, species check list, Moreton Bay, Queensland.*

Over the past decade our knowledge of the tropical Australian sponge fauna has increased substantially thanks to several major benthic surveys (e.g. http://www.reeffutures.org/topics/biodiversity/seafloor_second.cfm), and biodiscovery programs, searching for new compounds from nature with potential pharmaceutical properties (e.g. Quinn *et al.* 2002). These surveys have primarily focussed on Queensland waters including the coast, coral reefs and the inter-reef regions of the Great Barrier Reef, to the adjacent 'sea mounts' and off-shore reefs in the Coral Sea, and the Gulf of Carpentaria (e.g. Hooper *et al.* 2002). Prior to these surveys about 430 species had been described from these regions (Hooper & Wiedenmayer 1994), but since then over two thousand morphospecies have been collected, many thought to be new to science.

Amongst the families of Porifera, the family Raspailiidae is moderately diverse, within the class Demospongiae, containing 20 valid genera (one *incertae sedis*), seven subgenera, and approximately 250 named species worldwide, mainly from shallow waters and a few from abyssal depths (Hooper 2002; and literature therein). From this growing body of literature the Australian raspailiid fauna was assumed to be relatively well known, including a comprehensive taxonomic monograph (Hooper 1991), several subsequent papers on Australian and western Pacific islands faunas (Hooper & Lévi 1993; Hooper *et al.* 1999; Van Soest *et al.* 2006), several more dealing with other aspects of their biodiversity (Hooper & Lévi 1994; Hooper *et al.* 2000), and a synthesis of the family's systematic relationships and their morphological characteristics (Hooper 2002). Together these contributions have described a fauna of 59 species from Australian waters (including territorial seas) up to the present time, but only three species were previously recorded from the Moreton Bay region (Hooper 1991; Hooper & Lévi 1993; Van Soest *et al.* 2006).

Recent collections since the publication of Hooper (1991), particularly the comprehensive collection effort in 2005 during the 'Thirteenth International Marine Biological Workshop - The Marine Fauna and Flora of Moreton Bay', revealed another eight species of raspailiids living in this supposedly well known Moreton Bay fauna, including four new species described here.

Moreton Bay, including faunas inside the Bay and on the oceanic side of North Stradbroke and Moreton Islands, contains some of the most ecologically diverse environments on the east coast of Australia and a rich biota living in a biogeographic transition zone between tropical and temperate influences (Davie & Hooper 1998). Being adjacent to Brisbane (population circa 2 million) the area is probably under immense urban pressure, yet the fauna continues to reveal new discoveries despite many decades of collection effort. This present paper describes new species and records of the family Raspailiidae from this region, and an updated checklist of raspailiid species from Australia.

MATERIALS AND METHODS

Specimens were collected by SCUBA, trawls and scientific dredges, and are housed in the collections of the Queensland Museum. Only new material, published since the earlier revision of Australian Raspailiidae (Hooper 1991), is recorded here and readers are referred to that earlier publication for a full listing of examined material. Specimens were prepared for light and SEM microscopy using the usual methods (e.g. Hooper & Van Soest 2006). Spicule measurements are based on 30 spicules of each category and denoted as ranges (and means) of length x width. The systematic assignment follows the 'Systema Porifera' (Hooper & Van Soest 2002). Abbreviations used in the text: AIMS, Australian Institute of Marine Science; CSIRO, Commonwealth Scientific and Industrial Research Organisation; GBR, Great Barrier Reef, Queensland, Australia; NSW, New South Wales; NT, Northern Territory; NTM, Northern Territory Museum; Qld, Queensland; QM, Queensland Museum; WA, Western Australia.

SYSTEMATICS
Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885
Order Poecilosclerida Topsent, 1928
Suborder Microcionina Hajdu,
Van Soest & Hooper, 1994

Family **Raspailiidae** Nardo, 1833

Raspeliae Nardo, 1833.
Raspailiae Nardo, 1847.
Raspailiidae Hentschel, 1923.
Euryponidae Topsent, 1928.

Definition. Microcionina with a special category of smaller ectosomal styles, oxeas or anisoxeas forming discrete bouquets around the protruding larger styles or oxeas.

Remarks. Raspailiids are currently assigned to the Poecilosclerida but lack the primary apomorphy (chelae microscleres) of this order. They are assigned to the Microcionina based on similarities in morphological and some chemical features with the family Microcionidae in particular (refer to the synthesis provided by Hooper 2002). Genera are differentiated mainly on the basis of three morphological characters: (a) skeletal architecture ranging from axial compression to reticulate, plumo-reticulate or plumose skeletons; (b) the presence or absence of a specialised ectosomal skeleton (apomorphic for the family, whereby brushes of small ectosomal megascleres surround long protruding single choanosomal megascleres); and (c) geometric modifications to echinating megascleres. Full synonymies and diagnoses of all higher taxa are provided by Hooper (2002), with recent additions by Van Soest *et al.* (2006).

Subfamily **Raspailiinae** Nardo, 1833

Raspailia Nardo, 1833

Definition. Raspailiidae with a more-or-less compressed axial skeleton and a radial, plumose or simply reticulate extra-axial skeleton, with choanosomal spicules consisting of two, three or more different size classes (styles and/or oxeas), and echinating acanthostyles microcionid-like or secondarily modified.

Raspailia (*Raspailia*) Nardo, 1833

Definition. *Raspailia* with microcionid-like acanthostyles, myxillid-like acanthostyles or thin vestigial acanthostyles.
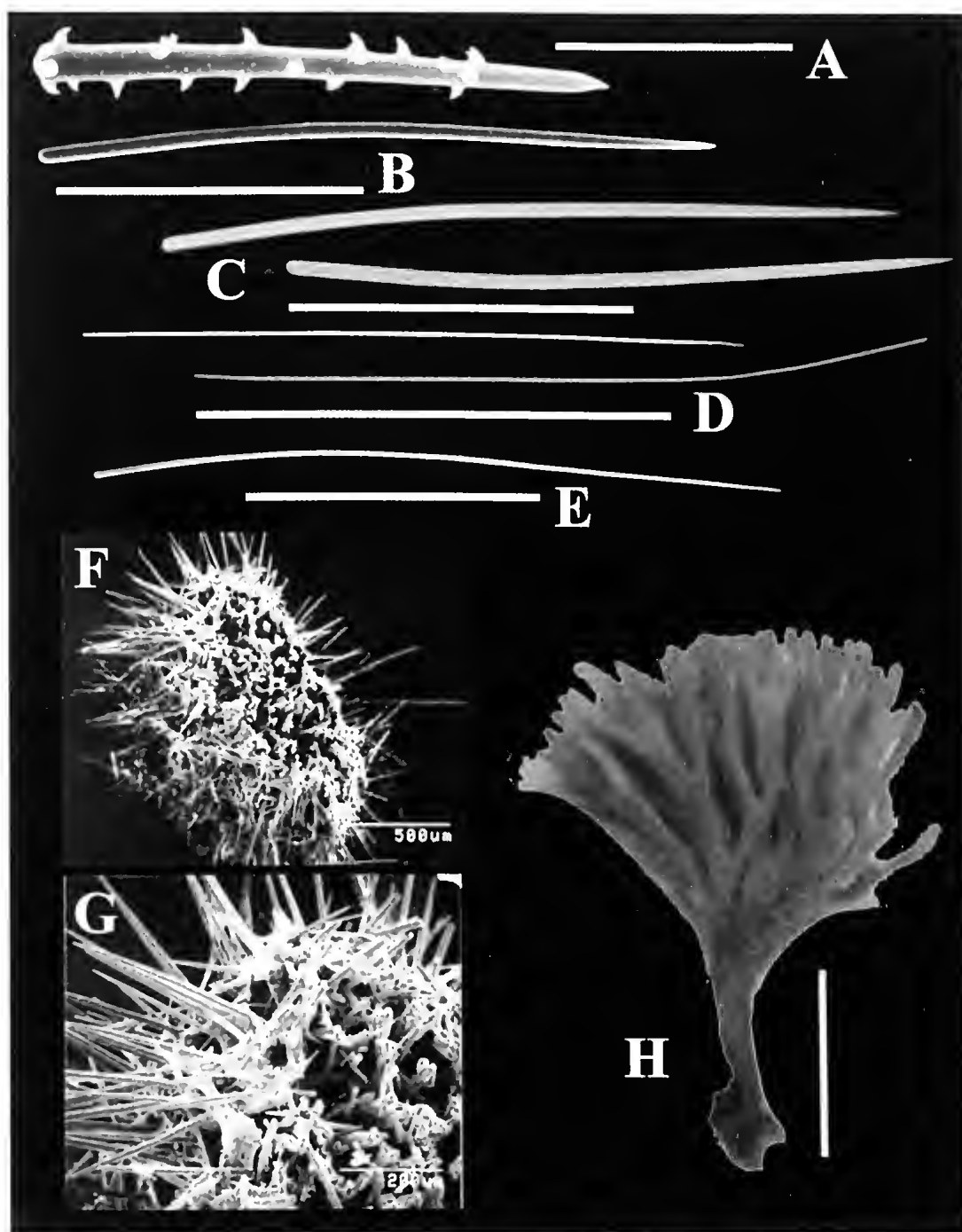
FIG. 1. *Raspailia (Raspailia) scorpa* sp. nov. (holotype QM-G315208). **A**, Echinating acanthostyles (scale bar 50 μm). **B**, Choanosomal style (scale bar 200 μm). **C**, Choanosomal styles (scale bar 200 μm). **D**, Ectosomal styles (scale bar 200 μm). **E**, Subectosomal style (scale bar 500 μm). **F**, SEM of skeletal structure, showing the axially compressed choanosome and radial subectosomal megascleres. **G**, SEM of ectosome, showing arrangement of ectosomal styles, radial echination of choanosomal styles and reticulation of choanosomal styles. **H**, Holotype (scale bar 2cm).

Raspailia (*Raspailia*) *scorpa* sp. nov.
(Figs 1, 2A, 8A, Table 1)

Material Examined. HOLOTYPE: QM-G315208, Green I., Moreton Bay, Qld, 27°25.5'S., 153°13.5'E., 4 m, 16.03.1999, coll. Marine Parks impoundment.

Habitat and Distribution. Coral rubble, 4 m depth range. So far known only from the type locality in Moreton Bay (Fig. 2A).

Description. *Shape.* Small arborescent sponge, approximately 5cm high, resembling a straw broom, with a dense crown of erect, flattened branches, many bifurcating several times at their tips. Branches occur in more than one plane giving a shrub-like appearance. Stalk is 1.8 cm long, 35–55 mm diameter, slightly flattened, firm, with basal holdfast. Branching occurs multiple times and occasionally fuses again towards the top. At the first bifurcation from the stalk the diameter ranges from 4–5 mm. When smaller branches (1.5–3 mm diameter) arise from this common base, they usually divide again 2–3 times, however they retain a similar width (23.5 mm) to the first branch. All branches are flattened equally, and range in thickness from 0.7–1 mm.

Colour. Deep red on deck, beige when preserved.

Oscules. Not observed.

Texture and surface characteristics. Firm but easily torn, slightly rubbery with flexible branches. Surface regular but very hispid.

Ectosome and subectosome. Ectosome exceptionally hispid as a result of protruding megascleres of several different categories, Subectosomal styles protrude through the surface up to 2 mm from the ectosome, in regular but sparse intervals. Shorter choanosomal styles protrude for only a small distance (<0.25 mm) through the ectosome but form a dense palisade-like surface layer. Ectosomal styles form a multispicular tangential layer arranged in tangential bundles around the point of insertion of subectosomal styles through the surface. Ectosome and subectosomal regions contain a well developed light brown layer of collagen in contrast to the choanosome which has only a very lightly collagenous mesohyl.

Choanosome. Choanosomal skeleton is axially compressed, consisting of a dense reticulation of choanosomal styles with only very few echinating acanthosyles visible. The choanosomal skeleton is dense and homogenous throughout the entire section (1.4–2.8 mm x 0.4–0.6 mm), surrounded by a subectosomal region ranging from 0.05–0.25 mm thick. Fibres are not well developed and mesohyl is clear, homogenous and lightly collagenous.

Megascleres (refer to Table 1 for dimensions). Ectosomal styles are very fine, sinuous, with evenly rounded bases and sharp points.

Subectosomal styles are very long, thin, usually sinuous, some with very slight subtylote swelling at the base but most evenly rounded bases.

Choanosomal styles are robust, curved at the centre or towards the basal end, most with sharply tapering points but some are slightly telescoped.

Echinating acanthostyles typically have a flattened, only slightly swollen base bearing several recurved spines arising at the very base of the shaft and forming a small clump. Spination along the shaft is very sparse, with a regular continuation of spines extending into the midsection, leaving the point bare. Spines with recurved hooks (3–4 μm long).

Remarks. *Raspailia* (*Raspailia*) *scorpa* sp. nov. is similar to *R.* (*R.*) *gracilis* (Lendenfeld) in gross morphology but differs in most other details (see Hooper 1991: 1206, Fig. 10). Conversely, despite differences in gross morphology *R.* (*R.*) *scorpa* is most similar to *R.* (*R.*) *phakellopsis* Hooper from the NT and northern WA in its skeletal structure and spicule composition, including the characteristic pattern of spination on echinating acanthostyles. In both species the subectosomal and choanosomal styles radiate in a similar fashion from the densely reticulate axial skeleton. However, the species clearly differ: *R.* (*R.*) *scorpa* has ectosomal styles (versus oxeas in *R. phakellopsis*), fewer and more robust and more recurved spines on the acanthostyles, and in the specific dimensions of most megascleres. *Raspailia phakellopsis* also has flattened convoluted leaf-like branches superficially resembling blades of brown alga (Hooper 1991), in contrast the straw broom-shaped growth form of the present species. There is also a contrasting arrangement of ectosomal styles, with *R.* (*R.*) *scorpa* having tangential bundles surrounding the protruding subectosomal styles, differing from *R. phakellopsis* which has erect bouquets or brushes typical of many raspailiids.

So far this species is known only from a single specimen from Moreton Bay, despite extensive surveys of the benthic faunas both north and south of this locality over the past decade. It is clearly a sister-species of *Raspailia phakellopsis*, which has a recorded distribution from Darwin, NT, and the Northwest Shelf, WA, both representing another example of east-coast/west-coast sister species pairs (Hooper 1991).

Etymology. This species is named for its broom-shaped gross morphology (L., *scorpa*, thin twigs, broom).

Raspailia (Raspailia) kennedyi sp. nov.
(Figs 2A, 3, 8B–C, Table 2)

Material Examined. HOLOTYPE: QM-G317177, Moreton Bay, off Toondah Harbour, Cleveland, Qld, 27°30.5'S, 153°18.1'E, 8 m, 2.viii.2000, J.A. Kennedy & T. Wassenberg.

Habitat and Distribution. The type specimen was collected from a seawater intake grate at a depth of 8 m. So far known only from the type locality in Moreton Bay (Fig. 2A).

Description. *Shape*. Large arborescent sponge on a single erect stalk (30 mm long) with round basal holdfast (13 mm diameter). First branching from the stalk is in one plane, with total branch span 15 cm wide. Numerous erect branches arise from the primary branches in the same plane and spread in one direction only. This may be as a direct result of the constricting sponge habitat (found growing on a grate and thus restricted in direction of growth). Branches separate many times in an irregular pattern and occasionally fuse again, creating a dense flattened shrub-like morphology. There appears to be no distinct pattern for fusion of branches except for proximity of branch growth. Branches have small forked distal tips. Branches vary in length, with the largest 12 cm long, and slightly flattened (25–54 x 21–42 mm). Total sponge height is 15cm.

Colour. Dark mauve-brown alive, darkening in air, and very dark brown in ethanol. Stains ethanol a light brown colour upon preservation.

Oscules. Minute (<1 mm) sparsely scattered along the sides of branches.

Texture and surface characteristics. Branches are flexible and compressible with a velvety feel, and easily torn. Surface is very hispid. The main stalk is very firm, almost woody, and not flexible.

Ectosome and subectosome. Dense bouquets of small ectosomal styles or anisoxeas protrude through the surface at regular intervals surrounding single large subectosomal styles, the latter protruding between 320–700 μm from the surface, visible with the naked eye and creating a very hispid surface. The subectosomal region has a layer of darkly pigmented layer of collagen (200–450 μm).

Choanosome. Strong axial compression with multispicular primary tracts of choanosomal styles. Secondary tracts usually lack spicules and consist only of spongin fibres, or some secondary tracts are unispicular. There is a high proportion of acanthostyles regularly echinating the primary tracts, and fibres are well developed and darkly pigmented.

Megascleres (refer to Table 2 for dimensions). Structural choanosomal styles are uniform and slightly curved at the centre, with evenly rounded bases and tapering to sharp points.

Subectosomal styles are long and thin, with evenly rounded bases, tapering sharp points, and slightly curved at centre or towards basal end.

Ectosomal styles or anisoxeas are short, very thin, straight or very slightly curved and difficult to see using light microscopy.

Echinating acanthostyles are short and robust, slightly subtylote bases, with small spines concentrated around the tip and covering the basal tyle and the neck of the shaft ranges from bare to lightly covered in short spines. Spines are erect near the basal end and slightly recurved towards the point, about 2 μm long,

Remarks. *Raspailia (Raspailia) kennedyi* sp. nov. is typical of the genus in its spicule composition and skeletal structure. The species is similar in shape (spiky surface, arborescent and multiple bifurcate branching, darkly pigmented) and ectosomal structure to *Raspailia vestigifera* Dendy from northern, northwest and central west Australia (see Hooper, 1991: 1215). Ectosomal brushes in both species are typically raspailiid, consisting of very fine styles (some verging on anisoxeas), forming bouquets around protruding single long subectosomal styles. The choanosomal region, however, is better developed in *R. (R.) kennedyi*, with multispicular primary tracts radiating to the surface and secondary spongin or unispic-
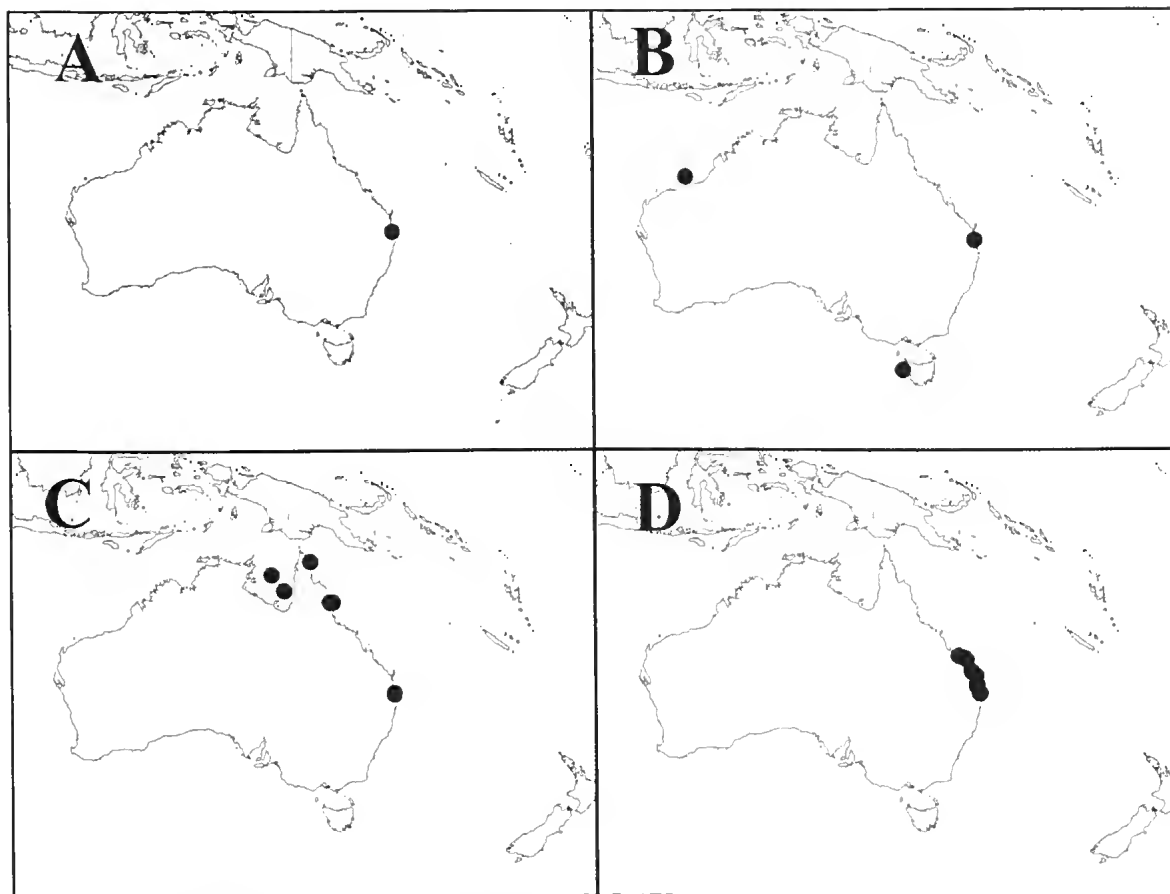
FIG. 2. Maps of wider distributions of *Raspailia* species found in Moreton Bay. **A**, *R. (Raspailia) scorpa* sp. nov. and *R. (Raspailia) kennedyi* sp. nov. **B**, *R. (Raspaxilla) compressa*. **C**, *R. (Parasyringella) australiensis*. D, *Aulospongus similiaustralis* sp. nov.

ular tracts of styles. Moreover, the choanosomal megascleres of *R. vestigifera* are strongylote and the species characteristically has few echinating acanthostyles, differing significantly from *R. (R.) kennedyi*.

Etymology. This species is named in appreciation of Mr John Kennedy, collector of the only known specimen of this species, and in recognition of his long and highly productive contributions to sponge biology at the QM.

Raspailia (Raspaxilla) Topsent, 1913

Definition. *Raspailia* with echinating rhabdostyles geometrically very different from the usually longer choanosomal styles (the latter without any basal rhabd); extra-axial styles forming a radial skeleton perpendicular to the axis; and well differentiated axial and extra-axial skeletons (the former compressed, the latter plumo-reticulate and/or radial).

Raspailia (Raspaxilla) compressa
Bergquist, 1970
(Fig. 2B, 8D)

Raspailia compressa Bergquist, 1970: 29–30, text-fig. 3a, pls 7b, 11a.
Raspailia (Raspaxilla) compressa — Hooper, 1991: 1245–1248, figs 32–33, table 6.
Material Examined. QM-G304878, South side Mud-jimba I., off Mooloolaba, Qld, 26°37.02'S, 153°6.15'E, 12 m, J.N.A. Hooper, J.A. Kennedy & S.D. Cook, 30.01.1995. QM-G323281, Pieman Canyon, Southeast Canyons, Tasmania, 41°44.38'S, 144°33.59'E, 176 m, A. Williams CSIRO RV 'Southern Surveyor' SS200404, dredge. Further material as listed in Hooper (1991).

Habitat and Distribution. 12–176 m, hard substrata. Known from North Cape, New Zealand
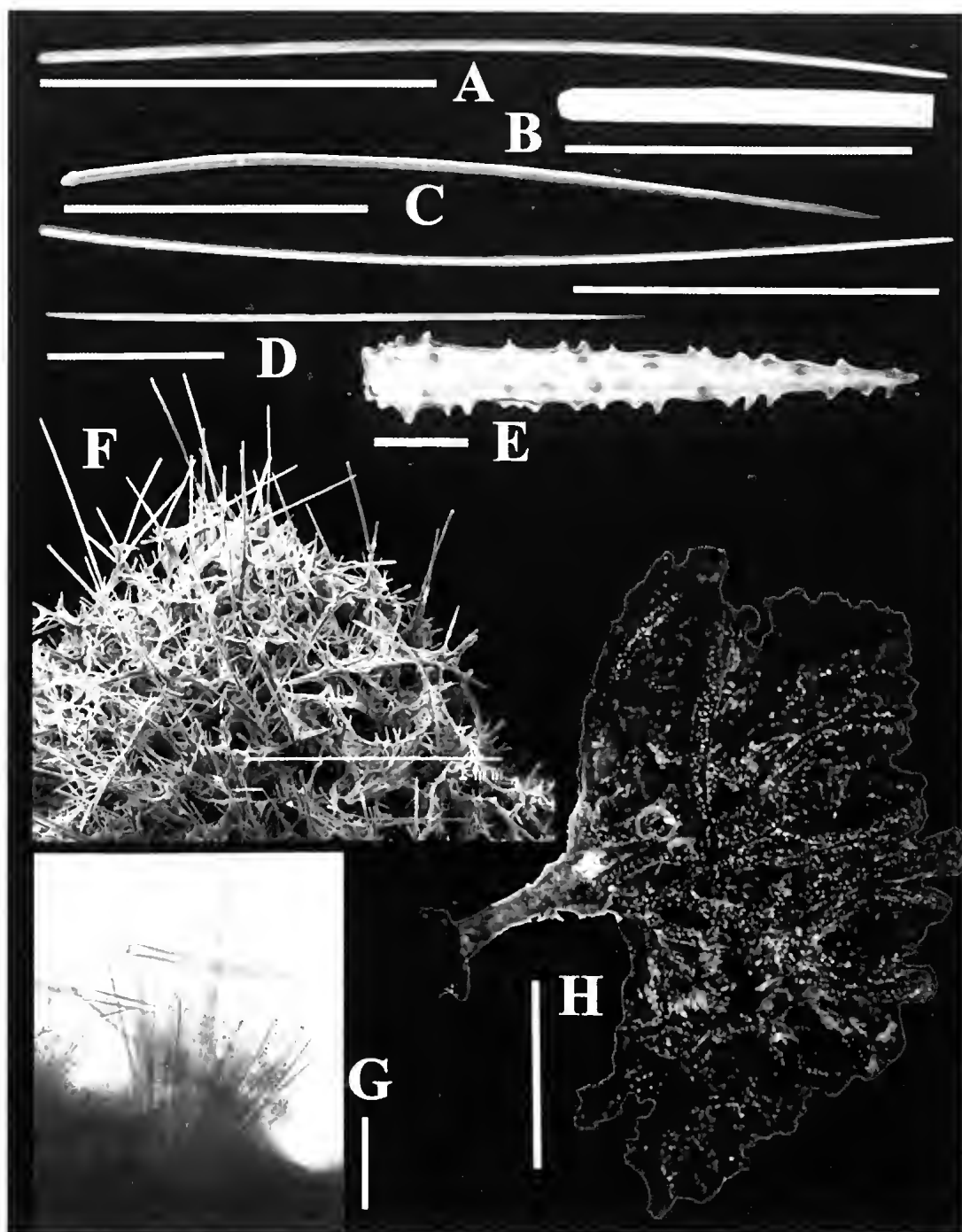
FIG. 3. *Raspailia (Raspailia) kennedyi* sp. nov. (holotype QM-G317177). **A**, subectosomal style (scale bar 500 μm). **B**, base of ectosomal style (scale bar 100 μm). **C**, choanosomal styles (scale bars 200 μm). **D**, ectosomal style (scale bar 100 μm). **E**, echinating acanthostyle (scale bar 10 μm). **F**, SEM of choanosome and ectosome, showing arrangement of styles in primary tracts and protruding subectosomal styles responsible for the hispid surface (scale bar 1 mm). **G**, light microscopy of bouquets of ectosomal styles surrounding a single subectosomal style (scale bar 100 μm). **H**, holotype on deck (scale bar 5 cm).

(type locality), Port Hedland region, WA, SE coast (Southeast Canyons), Tasmania, and the Moreton Bay region, SE Qld.

Remarks. This species was initially known only from the New Zealand type locality (Bergquist 1970), and subsequently comprehensively redescribed from deeper waters on the west coast of Australia (Hooper 1991). The new records reported here from deeper waters off the west coast of Tasmania and shallow waters in SE Queensland greatly extends the known range of this species, and indicates from these significantly disjunct distributions that it is probably a member of the temperate fauna, with the Moreton Bay record being a single incursion into subtropical waters, and that it is probably far more widely distributed than presently known. This species characteristically has an arborescent, bifurcating digitate growth form with cylindrical or slightly flattened branches, live colouration yellow-brown to olive-brown, an optically very hispid surface, and firm, barely compressible stalk with branches more flexible.

Raspailia (Parasyringella) Topsent, 1928

Definition. *Raspailia* which have secondarily lost their echinating megascleres.

Raspailia (Parasyringella) australiensis
Ridley, 1884
(Fig. 2C, 8F)

Raspailia (Syringella) australiensis Ridley, 1884: 460; Pick, 1905: 18, 35; Vosmaer, 1912: 316. Hooper, 1991: 1256–1259, figs 39–40, table 7.
Homaxinella australiensis — Burton, 1934: 42.

Material Examined. QM-G303010, NE Cape Grenville, Shelburne Bay, Qld, 11°55.03'S, 143°26.99' E, 51 m, S.D. Cook on FV 'Clipper Bird', 22.iii.1993, trawl. QM-G300814, E of Groote Eylandt, Gulf of Carpentaria, NT/Qld, 13°30.08'S, 138°47.08'E, 54 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 24.xi.1991, trawl. QM-G320826, Gulf of Carpentaria, Qld, 15°20.04'S, 140°19.83'E, 28 m, C. Bartlett & S.D. Cook on CSIRO RV 'Southern Surveyor' 2380403, 24.v.2003. trawl. QM-G320811, Gulf of Carpentaria, Qld, 15°20.03'S, 140°19.83'E, 28 m, C. Bartlett & S.D. Cook on CSIRO RV 'Southern Surveyor' 2380403, 25.v.2003, trawl. Further material as listed in Hooper (1991).

Habitat and Distribution. 7–54 m depth, on mud, sand or rubble substrates. Probably widely distributed in tropical north and north-east Australia, with confirmed records so far from Darwin, Northern Territory (type locality), Groote Eylandt NT and Gulf of Carpentaria, NT/Qld, northern section of the Great Barrier Reef to Moreton Bay, southern Qld (Fig. 2C).

Remarks. This species was comprehensively redescribed and illustrated in Hooper (1991), and is recognisable by its long stringy unbranched cylindrical growth form, muddy brown to whitish live colouration, its firm, flexible texture with a woody central stem and fleshy branches, and an optically even but microscopically rugose surface. It was originally recorded from Darwin (Ridley 1881), and subsequently from two other disjunct populations on the outer reefs on the northern section of the Great Barrier Reef, and the southern part of Moreton Bay (Macleay I.) in SE Queensland (Hooper 1991). The new material listed here from the inner far northern GBR and the Gulf of Carpentaria fills in the species' known, previously disjunct distribution.

Aulospongus Norman, 1878

Definition. Raspailiidae with at least two size classes of rhabdostyles of similar geometry, the larger (smooth or partially spined) core spongin fibres, and the smaller (partially spined) echinate fibres although neither are localised to any region of the skeleton; choanosomal skeletal structure is predominantly plumose, with spicules and fibres amalgamated into bulbous tracts ('fibre-bundles'), more-or-less compacted in the axial skeleton, becoming increasingly plumose as they ascend to the periphery, eventually producing a shaggy, compartmentalised or conulose surface; axial and extra-axial skeletons undifferentiated apart from greater amalgamation of fibre-bundles in the axis.

Aulospongus similiaustralis sp. nov.
(Figs 2D, 4, 8E, Table 3)

Material Examined. HOLOTYPE: QM-G300079, Shag Rock, SE Corner, North Stradbroke I., Qld, 27°24.5'S, 153°31.4'E, 15 m, 05.ii.1992, J.N.A. Hooper & J. Wilkinson, SCUBA. PARATYPES: QM-G315526, Western tip of Northwest I., Capricorn/Bunker Group, GBR, Qld, 23°18.4'S, 151°42.6'E, 15.7 m, 09.vi.1999, S. Cook *et al.* QM-G317317, Double Rock, Elliot Heads, Qld, 24°53.5'S, 152°29.3'E, 7.8 m, 11.x.2000, S.D. Cook *et al.* QM-G320085, southeast side, Outer Rock, Keppel Is, GBR, Qld, 23°3.5'S, 150°57.1'E, 15.8 m, 05.xi.2002, J.N.A. Hooper *et al.* OTHER MATERIAL. QM-G303218, Amity Pier and boat ramp, N Stradbroke I., 27°24.13'S,
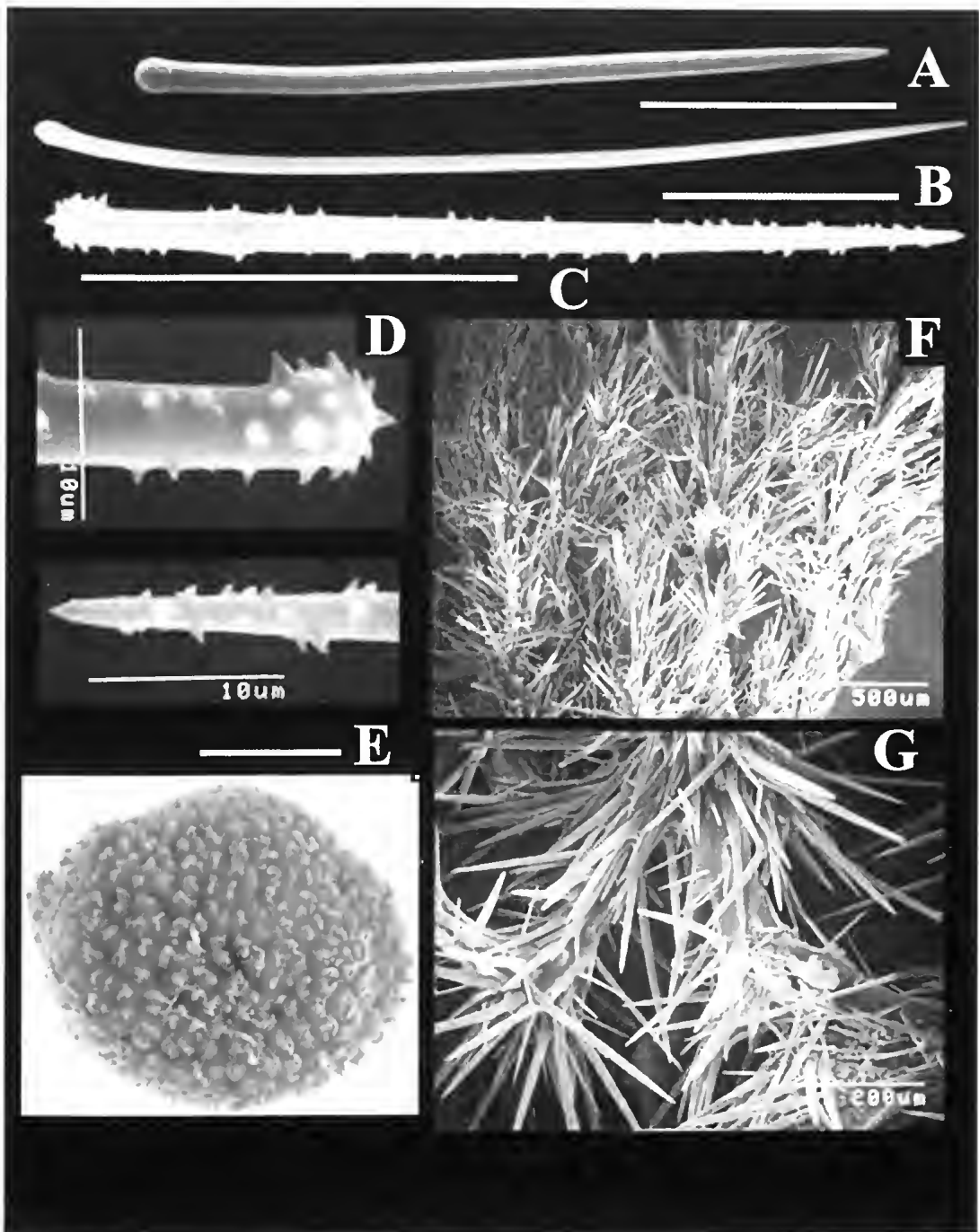
FIG. 4. *Aulospongus similiaustralis* sp. nov. (holotype QM-G300079). **A**, Choanosomal rhabdostyle with slight rhabd and distinct tyle (scale bar 100 µm). **B**, Subectosomal subtylostyle (scale bar 50 µm). **C**, Acanthostyle (scale bar 50 µm). **D**, Basal and distal spination of acanthostyle (scale bar 10 µm). **E**, Specimen (QM-G315610) top view (scale bar 5 cm). **F**, SEM of skeletal structure, showing the dense plumose fibre-bundles cored by choanosomal rhadostyles (scale bar 500 µm). **G**, SEM of choanosomal brush, showing arrangement of choanosomal styles and echinating acanthostyles (scale bar 200 µm).

153°25.08'E, 11 m, 10.xii.2003, J.N.A. Hooper & S.D. Cook. QM-G304007, north side, Mudjimba I., Mooloolaba, Qld, 26°36'.6 S, 153°6.8' E, 11 m, 09.ii.1994, J.N.A. Hooper *et al*. QM-G304879, South Side, Mudjimba I., Mooloolaba, Qld, 26°37' S, 153°6.8'E, 12 m, 30.i.1995, J.N.A. Hooper, J.A. Kennedy & S.D. Cook. QM-G303963, Jew Shoal, Noosa Heads, Qld, 26°21.9'S, 153°6.6'E, 20 m, 9.ii.1994, J.N.A. Hooper *et al*. QM-G315777, North Halls, Sunshine Coast, Qld, 26°20.4' S, 153°4.1' E, 21 m, 13.x.1999, S.D. Cook *et al*. QM-G315732, Jew Shoal, Noosa Heads, Qld, 26°22.3' S, 153°7.3' E, 18 m, 12.x.1999, S.D. Cook *et al*.. QM-G317276, Pandanas and Burkitt Points, Bargara, Qld, 24°48.2' S, 152°27.4' E, 6 m, 9.x.2000, S.D. Cook *et al*. QM-G306292, SW side of Little Woody I., Hervey Bay, Qld, 25°20'S, 153°1.5'E, 19 m, 18.xi.1995, J.N.A. Hooper *et al*. QM-G315610, eastern side of Wistari Reef, Capricorn Bunker Group, GBR, Qld, 23°28.5' S, 151°52.5' E, 15 m, 9.vi.1999, M. Garson, J. Simpson, & R. Clarke.

Habitat and Distribution. Coral reef, rock or rubble and sandy substrates, 6–21 m depth range. The known species range is from North Stradbroke Island, Moreton Bay, to the Keppel Is., Great Barrier Reef, Qld (Fig. 2D). Recently another single, so far unpublished, specimen of this species was recorded from the East Point Sponge Gardens, Darwin Harbour, NT (B. Alvarez pers. comm.) indicating a much more widespread distribution albeit very rare on the NW coast.

Description. *Shape*. Thickly encrusting globular, bulbous, spherical or subspherical sponges, ranging from 4–15 cm diameter and 2.5–6 cm. The globular growth form is composed of densely compartmentalised plumose columns, with columns flattened (24–36 x 0.5–1 mm) and arranged perpendicular to surface.

Colour. Bright orange; beige in preservative.

Oscules. Not observed.

Texture and surface characteristics. Velvety and compressible, can be torn easily. Surface is hispid and perpendicular columns of amalgamated spiculose fibre-bundles are inter-connected by a thin layer of spongin.

Ectosome and subectosome. No specialised ectosome is present although larger choanosomal rhabdostyles penetrate the surface arising from the underlying plumose fibre-bundles in the peripheral choanosomal skeleton. The dense arrangement of projecting rhabostyles produces a disorganised ectosome rather than a palisade-like structure typical of other raspailiids. Subectosomal subtylostyles are also organised in a plumose arrangement but they are sparsely distributed, predominantly in the peripheral skeleton. A darkly pigmented layer of collagen is present just below the surface, 100–150 μm thick.

Choanosome. Each perpendicular column arising from the choanosome to the peripheral skeleton consists of several bundles of amalgamated plumose fibre-bundles (each 50–100 μm in diameter), cored by multispicular tracts of choanosomal rhabdostyles coring and projecting from moderately heavy spongin fibres, and together with moderately abundant echinating acanthostyles form distinctly plumose ascending columns, 300–600 μm in diameter, without any apparent reticulate spicule or fibre interconnections. Spicules are dense and project obliquely from fibres. Long, thin subectosomal subtylostyles project from columns only sparsely. Lightly pigmented collagen is distributed throughout the choanosome.

Megascleres (refer to Table 3 for dimensions). Choanosomal rhabdostyles are robust, tapering to sharp points, only slightly rhabdose at the base with curvature proximal to the base. The basal tyle is typically swollen with a subtylote constriction, less often without pronounced swelling and only faint curvature.

Subectosomal subtylostyles are long, thin, often curved at the centre or towards the basal end, with the basal subtylote swelling small but with a pronounced subtylote constriction, and slightly rhabdose base.

Echinating acanthostyles are long, slender, prominently subtylote, with only a very faint rhabdose basal curvature. Small spines evenly distributed along the shaft except for a bare point, and basal tile covered with small spines. Spines are erect or slightly recurved, and less than 1 μm long.

Remarks. In its superficial growth form (encrusting bulbous, globular), surface features (conulose or papillose), live colouration (orange or red), possession of slightly rhabdose megascleres, and choanosomal structure (bundles of perpendicular spicule tracts) this species is remarkably superficially similar to *Dragmacidon australe* (Bergquist, 1970) (Halichondrida: Axinellidae). However, these similarities are purely convergent as demonstrated by differences in spicule composition between the two species (with *D.*

australe having only styles and oxeas, the former slightly rhabdose). Another superficial comparison is with *Dragmaxia variabilis* (Whitelegge) (Halichondriidae), which has a similar skeletal structure consisting of skeletal columns with spicules obliquely directed towards the surface, but the principal spicules in *A. similiaustralis* are distinctly plumose in formation, choanosomal styles and echinating acanthostyles are both rhabdose (albeit with poorly developed rhabds), and *D. variabilis* also contains trichodragmata and raphides. The new species clearly belongs to *Aulospongus* in having dense plumose fibre-bundles cored by rhabdostyles forming ascending columns, closely arranged at the base of the sponge, and separating completely towards the surface of the sponge, or into compartments, and structural styles and echinating acanthostyles of similar geometry, both characteristic for the genus. In contrast, other raspailiids with rhabdostyles, *Raspailia (Raspaxilla)*, have choanosomal principal styles geometrically different from echinating acanthostyles, the choanosomal principal styles lack any basal rhabd, and there are no discrete ascending fibre-bundles forming columns but instead with well differentiated axial and extra-axial skeletons (Hooper 2002).

The present species is most similar to *A. tubulatus* (Bowerbank, 1873), described from the western Indian Ocean to Sri Lanka, in possessing discrete surface conules produced by fibre-bundles and columns, a red or pinkish live colouration, and both having poorly developed rhabdose bases on both choanosomal rhabdostyles and echinating acanthostyles. The two species differ in other aspects, with *A. tubulatus* having some reticulate aspicular fibres interconnecting ascending columns, a massive tubular or subspherical growth form, lacking subectosomal styles but having instead smaller ectosomal rhaphiform styles, and patterns of spination and specific dimensions of spicules differing substantially (Table 3) (Hooper *et al.* 1999). In its spination *A. similiaustralis* is unusual amongst *Aulospongus* in having echinating acanthostyles more or less completely and evenly spined (similar to *Raspailia* species), whereas these spicules in most *Aulospongus* species have a smooth base and spined only or predominantly on the distal part of the shaft and point. Refer to Hooper *et al.*

(1999) for a comparison with other known species of *Aulospongus*.

Etymology. This species is named for its remarkable superficial resemblance to *Dragmacidon australe* (Bergquist, 1970), formerly allocated to *Pseudaxinella*.

Sollasella Lendenfeld, 1887

Definition. Raspailiidae with strong axial column of confusedly aligned oxeas and styles, and with extra-axial columns of short oxeas and long and short styles positioned at right angles to the axial column. At the surface there is a characteristic ornamentation of polygonally arranged inhalant (?) pores and the oxeas form a continuous palisade of brushes of oxeas pierced by long styles. A low proportion of short acanthostyles may be present.

Sollasella moretonensis Van Soest et al., 2006
(Fig. 5A, 9A)

Sollasella moretonensis Van Soest, Hooper, Beglinger & Erpenbeck, 2006: 140–143, figs 4–5, Table 2.

Material Examined. Specimens as listed in Van Soest *et al.* (2006).

Habitat and Distribution. This species is moderately common in waters outside and adjacent to Moreton Bay, extending up to Noosa on the Sunshine Coast, associated with muddy substrata at the base of coral reefs, with a known depth range of 11–31 m (Fig. 5A).

Remarks. All known material of this species was recently described and published by Van Soest *et al.* (2006), with the holotype (QM-G303227), paratype and six specimens collected from the eastern side of North Stradbroke I. (type locality, 27.40083°S, 153.53°E) up to the northern end of the Sunshine Coast (26.3461°S, 153. 067°E), one from Shelburne Bay, north Qld (11.61722°S, 143.06889°E), and one very disjunct specimen from the vicinity of Cape Jaubert, north coast of WA (19.76667°S, 118.21667°E). As noted in Van Soest *et al.* (2006), the two isolated records in Shelburne Bay and Cape Jaubert were from commercial and scientific trawls made in deeper muddy substrates, and suggest that the species may have a wider distribution than presently known, or a disjunct distribution in tropical Australia, although this pattern is still unclear given that there has been intensive sampling of areas in between without trace of this species.

The species is very distinctive morphologically. It is bright orange to orange-brown in life, with a vasiform to fan-shaped growth form bearing rounded 'lumpy' margins, usually attached to the substrate by a short cylindrical woody hold-fast. Texture is harsh, slightly hispid, firm and stiff, and the surface has a distinctive polygonal plate-like pattern formed by shallow pits surrounding low conules, each perforated by an oscule with a raised lip at its apex, pigmented more darkly than the surrounding area, and reminiscent of typical *Polymastia* surface patterns.

Subfamily Thrinacophorinae Hooper, 2002

Ceratopsion Strand, 1928

Definition. Raspailiidae lacking echinating spicules, having an axially compressed choanosomal skeleton with reticulate fibres cored by sinuous styles or anisoxeas and a well differentiated radial extraaxial skeleton cored by longer megascleres.

Ceratopsion clavatum Thiele, 1898
(Fig. 5B, 9B)

Ceratopsis clavata Thiele, 1898: 57, pl.5, fig.23, pl.8, fig.42a–c.
Ceratopsion clavata – Hooper, 1991: 1328, table 18. Hooper & Lévi, 1993: 1287–1291, figs 35–37, table 15.
Material Examined. NORTHERN NSW: QM-G301426, The Nursery/ Cod Hole, NE of Julian Rocks, Byron Bay, 28°36.13'S, 153°37.12'E, 17m, J.N.A. Hooper & S.D. Cook, 3.ii.1993. SOUTHEAST QLD: QM- G301289, Hanlon Light, Moreton Bay, 27°28.5'S, 153°20.9'E, 10 m, J.N.A. Hooper & S.D. Cook, 3.xi.1992. QM-G303975, North side of Mudjimba I., off Mooloolabah, 26°36.12'S,

153°6.15'E, 11 m, J.N.A. Hooper *et al.*, 9.ii.1994. QM-G320226, precise locality unknown, Deception Bay, Moreton Bay, Qld, QDPI Fisheries, FV 'Southern Intruder' Scallop Survey, 11.x.2002, trawl. GREAT BARRIER REEF, QLD: QM-G303862, S Triangle Reef, Hook Reef, Whitsunday region, 19°49.03'S, 149°7.02'E, 28 m, J. Hooper & L.J. Hobbs, 9.xii.1993. QM-G304371, NW of Lizard I., W. of Underwood Shoal, 14°35.02'S, 145° 20.13'E, 24 m, DPI on FV 'Gwendoline May', 9.iv.1994, trawl. QM-G320714, Mid Reef, Howick Group, 14°26.89'S, 144°52.88'E, 23 m, J. Hooper, *et al.*, 3.vii.2003. QM-G320792, Houghton Reef, Howick Group, 14°31.19'S, 144° 58.89'E, 20 m, J.N.A. Hooper *et al.*, 3.vii.2003. QM-G304918, QM-G304916, precise locality unknown, N. Coleman, 13.v.1994. QM-G306716, Petricola Shoals, NE. of Lizard I., 14°37.13'S, 145°28.08'E, 23 m, J. Hooper & P.A. Tomkins, 6.iii.1996. CORAL SEA TERRITORIES, off QLD: QM-G320588, Wilson Reef, 13°40.36'S, 144°13.59'E, 36 m, J.N.A. Hooper *et al.*, 1.vii.2003. QM-G320634, Davie Reef, 13°59.22'S, 144°26.47'E, 23m, J.N.A. Hooper *et al.*, 1.vii.2003. QM-G320685, Munro Reef, 14° 18.15'S, 144°48.81'E, 23 m, J.N.A. Hooper *et al.*, 2.vii.2003. PAPUA NEW GUINEA: QM-G312952, Keppel Point, Hood Bay, SE Papuan Lagoon, 10°8.13'S, 147° 54.15'E, 35 m, J.N.A. Hooper & M. Kelly, 16.xii.1996. QM-G312936, 12 mile sandbank, Kupiano, SE Papuan Lagoon, 10°11.05'S, 148°10.13'E, 20 m, J.N.A. Hooper & M. Kelly, 15.xii.1996. Further material as listed in Hooper (1991) and Hooper & Lévi, (1993).

Habitat and Distribution. Coral and rock substrates, 10–130 m depth (deeper samples from New Caledonia). Possibly very widely distributed in the tropical and subtropical Indo-west Pacific although so far only with confirmed distributions reported from Sagami Bay, Japan (type locality), south-west lagoon of New Caledonia (Hooper & Levi 1993), Southern Papua New Guinea Barrier Reef, Coral Sea territories, Great
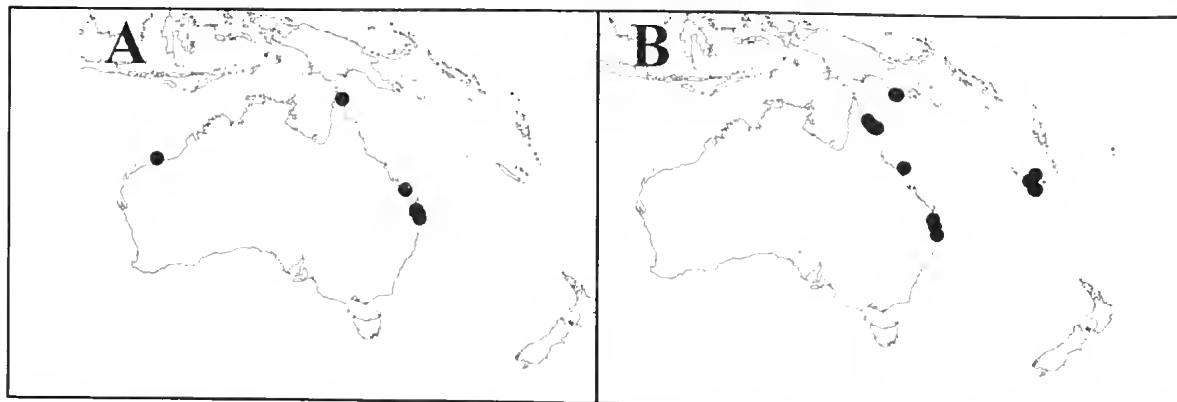
FIG. 5. Maps of wider distributions of raspailiid species found in Moreton Bay. **A**, *Sollasella moretonensis*. **B**, *Ceratopsion clavata*.

Barrier Reef, South East Qld to northern NSW (present study) (Fig. 5B).

Remarks. This species is well-recognisable by its yellow to pale orange colouration in life, an arborescent digitate morphology ranging from bushy to elongate digitate or whip-like, and a prominently conulose surface. It was comprehensively redescribed by Hooper & Lévi (1993) from New Caledonian and Moreton Bay specimens, with the present study greatly extending its known distribution from southern PNG to subtropical eastern Australia.

Subfamily Echinodictyinae Hooper, 2002

Echinodictyum Ridley, 1881

Definition. Raspailiidae with an exclusively reticulate choanosomal skeleton, without any trace of axial compression, cored exclusively by smooth oxeas, and vestigial radial extra-axial and ectosomal skeletons.

Echinodictyum asperum Ridley & Dendy, 1886
(Fig. 6A, 9C)

Echinodictyum asperum Ridley & Dendy, 1886: 477. Ridley & Dendy, 1887: 165, pl.32, fig.2; Whitelegge, 1897: 328–329; Topsent, 1897: 446, pl.20, fig.23; Burton & Rao, 1932: 348; Lévi, 1961: 524, fig.15; Desqueyroux-Faundez, 1981: 757, table II; Hooper, 1984: 55; Hooper, 1991: 1353-1356, figs 86-87, 110c, table 20.

Material Examined. MORETON BAY REGION, QLD: QM-G303197, Conjevoi Reef, off Sovereign Beach, east of Moreton I, 27°16.13'S, 153°25.08'E, 14 m, J.N.A. Hooper & S.D. Cook, 1.vi.1993. GREAT BARRIER REEF, QLD: QM-G314132, Lady Musgrave I., inside lagoon wall near entrance, 23°53.99'S, 152°24.62'E, 11 m, J.N.A. Hooper *et al.*, 25.ii.1998. FAR NORTH QLD: QM-G303055, NE Cape Grenville, Shelburne Bay, 11°40.03'S, 143°4.03'E, 28 m, S.D. Cook on FV 'Clipper Bird', 25.iii.1993, trawl. QM-G303064, NE Cape Grenville, Shelburne Bay, 11°25.13'S, 143°52.03'E, 23 m, S.D. Cook on FV 'Clipper Bird', 27.iii.1993, trawl. QM-G316939, Torres Strait, 10°24.6'S, 142°41.40'E, 20 m, C. Bartlett on RV 'Gwendoline May', 13.i.2004, trawl. NORTHERN TERRITORY: QM-G303358, Stephen's Rock, West Arm, Darwin Harbour, 12°29.17'S, 130°47.18'E, 19 m, J.N.A. Hooper & L.J. Hobbs, 24.ix.1993. QM-G310228, Darwin Harbour, 12°17.58'S, 130°28.44, 13 m, Australian Institute of Marine Science NCI group, 20.viii.1987. QM-G313317, North of Bathurst Is, Arafura Sea, 11°19.98'S, 130°12.18'E, depth unknown, T. Wassenberg, CSIRO, 10.iii.1997, dredge. QM-G303566, Vernon Is, SSE of

Lyne Reef, 12°7.0'S, 130°59.0'E, 30 m, Conservation Commission of the Northern Territory, 11.x.1993, dredge. QM-G301203, Flattop Bank, NE Joseph Bonaparte Gulf, Timor Sea, 12°16.0'S, 129°15'E, 32 m, J.N.A. Hooper, 17.v.1992, dredge. WESTERN AUSTRALIA: QM-G306039, NE of Dampier, 19°14.12'S, 117°36.10'E, 98 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 1.ix.1995, dredge. PALAU ISLANDS: QM-G306396, QM-G306397, Kaibakku Tunnel, Ngeteklou, 7°19.08'N, 134°29.0'E, 8 m, J.N.A. Hooper, 14.xii.1995. FEDERATED STATES OF MICRONESIA: QM-G301245, Mortlock Is, Etal Atoll, NE section of lagoon, Chuuk, 5°34.09'N, 153°33.05'E, 22 m, Coral Reef Research Foundation, 9.vi.1992. Further material as listed in Hooper (1991).

Habitat and Distribution. This species is mostly found associated with hard rock and dead coral substrates, from subtidal to deeper water reefs (6–96 m depth). It is widely distributed from Tahiti to India, and from Chuuk Atoll to southeast Qld (Fig. 6A).

Remarks. This species has a wide distribution within the tropical Indo-west Pacific, with specimens examined from Papiete, Tahiti (type locality) (Ridley & Dendy 1886, 1887), to Tuticorin, India (Burton & Rao 1932), Tuvalu (Whitelegge 1897), Indonesia (Topsent 1897; Desqueyroux-Faundez 1981), Philippines (Lévi 1961), northwest Australia and Northern Territory (Hooper 1991), Chuuk, Palau and along the northeast coast of Australia from Torres Strait to the Moreton Bay region (present study). This is the first record of this species from the east coast of Australia. Interestingly, there is not yet any confirmed record of this species within the Gulf of Carpentaria, despite some significant sampling effort there, with an apparently disjunct distribution of western (west of the Wessel Islands, NT) and eastern populations (southeast of the Torres Straits, Qld). The species is characterised by a light brown to grey brown live colouration, with honeycomb-like dense reticulation of flattened branches forming spherical or irregular lobate masses, occasionally arborescent, with a firm, compressible but difficult to tear texture, and an optically uneven surface that is cavernous from the close-meshed reticulate branches.

Echinodictyum conulosum Kieschnick, 1900
(Fig. 6B, 9D)

Echinodictyum conulosum Kieschnick, 1900: 570–1. Hooper, 1991: 1370–1373, figs 95–96, 110h, table 24.
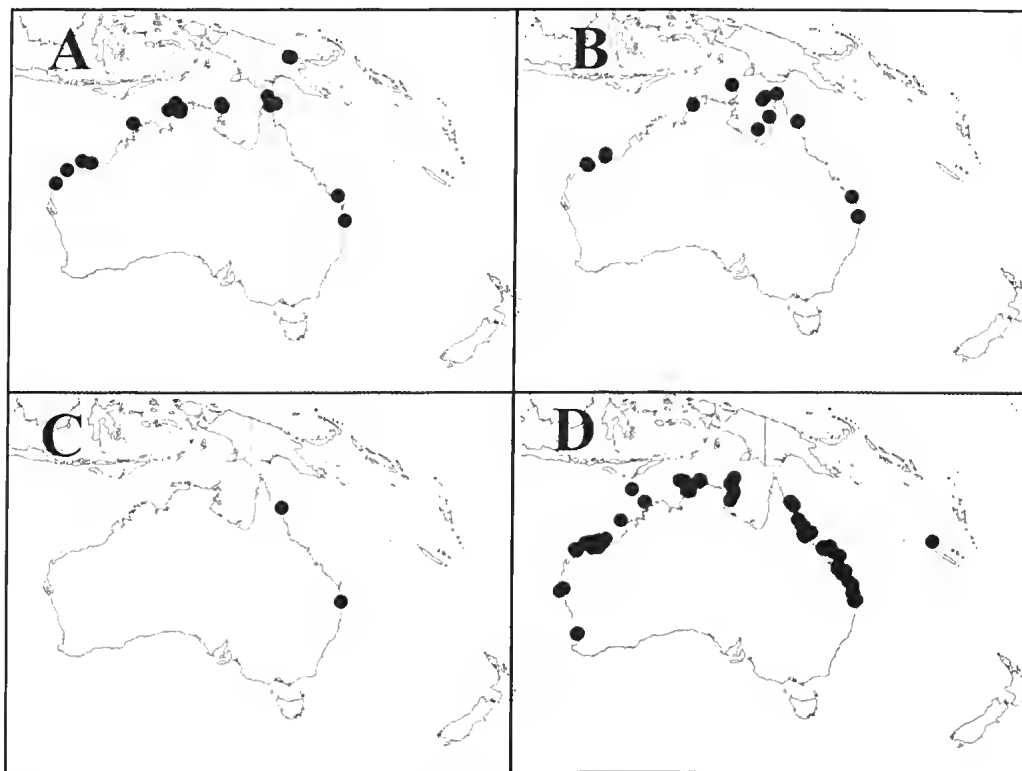
FIG. 6. Maps of wider distributions of *Echinodictyum* species found in Moreton Bay. **A**, *E. asperum*. **B**, *E. conulosum*. **C**, *E. luteum* sp. nov. **D**, *E. mesenterinum*.

Material Examined. SOUTHEAST QLD: QM-G317169, off Toondah Harbour, Cleveland, 27°30.91'S, 153°18.19'E, 8 m, J.A. Kennedy & T. Wassenberg, 2.viii.2000. QM-G317228, Myora Light, west side of North Stradbroke I, Moreton Bay, 27°28.10'S, 153°24.07'E, 1 m, J.N.A. Hooper, 26.ix.2000. QM-G320278, Wellington Point, Moreton Bay, 27°30'S, 153°15'E, 1 m, S.A. List-Armitage, 15.iv.2003. CENTRAL QLD: QM-G317265, inshore reef at Pandanas and Burkitt Points, Bargara, 24°48.47'S, 152°27.72'E, 6 m, S.D. Cook *et al.*, 9.x.2000. FAR NORTH QLD: QM-G321041, Torres Strait, 10°51.0'S, 142°7.8'E, 16 m, C. Bartlett on FV 'Gwendoline May', 9.xi.2004, trawl. Further material as listed in Hooper (1991).

Habitat and Distribution. Shallow coastal and shallow offshore rock reefs, in mud or areas with high sedimentation rates; 1–84 m depth. Tropical and subtropical distribution from the Port Hedland region, WA, around to SE Qld (Fig. 6B).

Remarks. Even though Kieschnick's (1900) paper concerned species mainly from Ambon, Indonesia, the label on the holotype in the Phyletisches Museum in Jena, Germany (PMJ POR85) indicates that it was collected from Thursday I., Torres Strait. It was subsequently redescribed from extensive collections from mainly inshore turbid localities extending from the Northwest Shelf of WA, Darwin, NT, Gulf of Carpentaria, Qld, to the inner GBR, Qld (Hooper 1991). Present records extend this distribution substantially along the northeast coast of Australia to Moreton Bay, Qld. The species is jet black or black with a purple tinge when alive, usually silt covered in shallow water specimens, and has a cavernous reticulate growth form typical of *Echinodictyum* being elongate, conical, lobate or digitate, with short basal stalk. The texture is firm and flexible, and the surface is covered with numerous large conulose projections with pointed furry tips.

Echinodictyum luteum sp. nov.
(Figs 6C, 7, 9E, Table 4)

Material Examined. HOLOTYPE: QM-G304769, Nymph I., West of Lizard I., Great Barrier Reef, Qld, 14°39.0'S,

145°13.1'E, 17 m depth J.A. Kennedy, DPI Fisheries FV 'Gwendolyn May', 04.ix,1994, trawl. PARATYPES: QM-G317152, off Toondah Harbour, Cleveland, Moreton Bay, Qld, 27°30.91'S, 153°18.19'E, 8 m, J.A. Kennedy & T. Wassenberg, 02.viii.2000. QM-G306395, Kaibakku Tunnel Ngeteklou, Palau 7°19.08'N, 134°29.0'E, 8 m, J.N.A. Hooper, 14.xii.1995.

Habitat and Distribution. Found on rocky substrate and sheltered overhangs, from 8–17 m depth. The species is rare and the three known specimens are widely disjunctly distributed, from Moreton Bay, SE Qld, the northern Great Barrier Reef and Palau (Fig. 6C).

Description. *Shape.* Stalked, with a small basal attachment (1–3 cm long, up to 1 cm in diameter) and shrub-like body composed of partially or fully fused anastomosing branches, forming a close-meshed reticulate club or fan (6–14 cm high, 8–13 cm wide).

Colour. Yellow to yellow-brown both in life, and in ethanol, which it stains a light yellow.

Oscules. Not observed.

Texture and surface characteristics. Soft, fleshy and compressible sponge with cavernous reticulate structure. Tips of conules thrown up into points which give shaggy appearance, and are easily torn.

Ectosome and subectosome. Ectosome membranous, without any specialised raspailiid skeleton, but with a tangential layer of oxeas in sparsely confused arrangement lying immediately below the ectosome.

Choanosome. Primary and secondary tracts are multispicular and form an irregular yet well-defined reticulation with cavernous meshes. Individual oxeas are scattered throughout the choanosome within a lightly collagenous mesohyl. Primary and secondary tracts are regularly echinated by long slender acanthostyles.

Megascleres (refer to Table 4 for dimensions). Primary oxeas are long and thick, slightly curved centrally, with tapering sharp points.

Secondary oxeas are significantly thinner, less prominently curved than primary oxeas, and with blunter points.

Echinating acanthostyles are long, slender, mostly straight, with a slight subtylote swelling. Pattern of spination varies along the length of the spicule, being light and regular on the shaft, becoming more concentrated at the base and tip. Base is covered in clumped blunt and sharp spines, mostly erect, few recurved. The neck, below the tyle, has fewer erect sharp spines and few small blunt spines. Spination decreases in the upper-midsection of the shaft where they are erect and pointed, and then increases to larger recurved thorny spines along the lower-midsection and these continue to the point. The larger spines are up to 3 μm long.

Remarks. *Echinodictyum luteum* sp. nov. is unusual within the genus in its live yellowish colour, whereas most species are darkly pigmented (black, purple, dark brown), including a heavily pigmented mucus (Hooper 1991). This species also has characteristic long, slender and peculiarly spined acanthostyles, with spination varying from sharp and erect on the basal end to strongly recurved and thorny on the distal end. The morphology of acanthostyles was found to be a useful character to differentiate species of *Echinodictyum*, in an otherwise fairly homogeneous and morphologically depauperate group of sponges (Hooper 1991). In this character *E. luteum* sp. nov. is marginally most similar to *E. clathratum* Dendy from the Indian Ocean. Hooper (1991) provides a synopsis and illustrations of all known *Echinodictyum* species.

The significant disjunct distribution of this species from southeast Queensland, the Great Barrier Reef and Palau is also remarkable, and the species appears to be rare, with the assumption that it may occur in between this extensive geographic ranges. The only notable difference between Queensland and Palau specimens is the latter has marginally larger acanthostyles (Table 4).

Etymology. This species is named for its unusual colouration (from Latin *luteus*, yellow).

Echinodictyum mesenterinum (Lamarck, 1814)
(Fig. 6D, 9F)

Spongia mesenterina Lamarck, 1814: 444.
Echinodictyum mesenterinum — Carter, 1882: 114; Ridley, 1884b: 185; Topsent, 1932: 101; Hooper, 1984: 55; Hooper, 1991: 1379–85, figs 100–103, 110i, table 25.
Spongia bilamellata Lamarck, 1816: 436 (in part, var. á).
Echinodictyum bilamellatum —Ridley, in Ridley & Duncan, 1881: 493, pl. 28, figs 1–6; Ridley, 1884: 454; Hentschel, 1911: 385; Hallmann, 1912: 299,
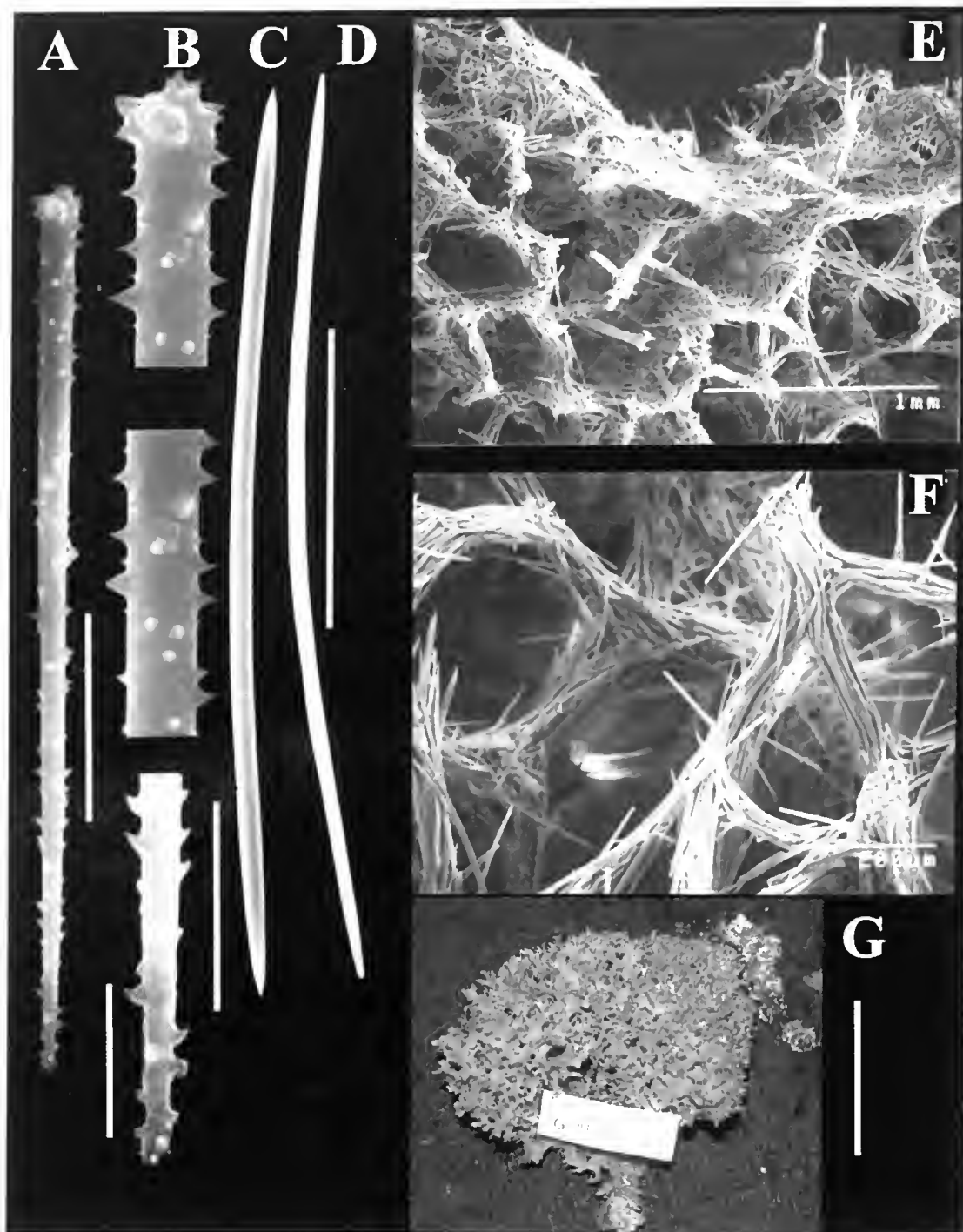
FIG. 7. *Echinodictyum luteum* sp. nov. (holotype QM-G304769). A, Echinating acanthostyle (scale bar 25 μm). B, Spination pattern on echinating acanthostyle (scale bar 10 μm). C, Primary choanosomal oxea (scale bar 100 μm). D, Secondary choanosomal oxea (scale bar 100 μm). E, SEM of skeletal structure, showing reticulation of multispicular tracts (scale bar 1 mm). F, SEM of choanosome, showing arrangement of oxeas and echination of acanthostyles (scale bar 200 μm). G, holotype on deck (scale bar 8 cm).

1914: 267; Dendy & Frederick, 1924: 504; Topsent, 1932: 69, 101, pl. 6, fig. 5; Topsent, 1933: 23; Burton, 1938: 15, 20; Guiler, 1950: 7.

Kalykenteron elegans Lendenfeld, 1888: 216; Hallmann, 1914: 267.

Echinodictyum elegans – Hallmann, 1912: 171, pl. 23, fig. 1, text-fig. 35.

Kalykenteron silex Lendenfeld, 1888: 217; Hallmann, 1914: 267.

Echinodictyum topsenti de Laubenfels, 1936: 63.

Thalassodendron typica – Whitelegge, 1901: 86 (in part); Hallmann, 1912: 171, 203. [Not *Thalassodendron typica* Lendenfeld, 1888: 233].

Echinonema vasiplicata Carter, 1882: 114; Ridley, 1884: 454; Hentschel, 1911: 385.

Material Examined. SOUTHEAST QLD: G315659, Sunshine Reef, Sunshine Coast, 26°24.77'S, 153°8.08'E, 27 m, S.D. Cook *et al.*, 11.x.1999. QM-G300883, Myora Reef, North Stradbroke I., Moreton Bay, 27°28.08'S, 153°24.10'E, 8 m, J. Hooper & S. Cook, 14.iv.1992. QM-G301280, off Banana Bouy to Pat's Point, 27°33.08'S, 153°20.05'E, 3 m, K. Lamprell, M. Norman & C. Eddie, 1.x.1992, dredge. QM-G301303, E. side Peel I., Moreton Bay, 27°30'S, 153°24.0'E, 3 m, J. Hooper & S. Cook, 3.xi.1992. QM-G301304, Myora Light, W side North Stradbroke I., 27°28.10'S, 153°24.07'E, 4 m, J. Hooper & S. Cook, 3.xi.1992. QM-G303222, 1.85 nm off Peel I., 3.8 nm off Cleveland, Moreton Bay, 27°28.10'S, 153°20.08'E, 10 m, J.N.A. Hooper & S.D. Cook, 3.vi.1993, trawl. QM-G303238, Middle Reef, nth of North Stradbroke I., 27°24.05'S, 153°31.99'E, 30 m, J.N.A. Hooper & J.A. Kennedy, 4.vi.1993. QM-G313405, QM-G313409, Dunwich, North Stradbroke I., 27°30'S, 153°24.0'E, 1 m, S.D. Cook, 18.viii.1997. QM-G317154, QM-G317168, off Toondah Harbour, Cleveland, 27°30.91'S, 153°18.19'E, 8 m, J.A. Kennedy & T. Wassenberg, 2.viii.2000. QM-G320272, Wellington Point, Moreton Bay, 27°30'S, 153°15'E, intertidal, S. List-Armitage *et al.*, 15.iv.2003. QM-G303998, QM-G304004, N side of Mudjimba I., off Mooloolabah, Sunshine Coast, 26°36.12, 153°6.15'E, 11 m, J.N.A. Hooper *et al.*, 9.ii.1994. QM-G315107, Outer Gneerings, Sunshine Coast, 26°39.45'S, 153°12.89'E, 28 m, J.N.A. Hooper *et al.*, 15.x.1998. QM-G303959, Jew Shoals, Noosa Heads, Sunshine Coast, 26°21.15'S, 153°6.10'E, 20 m, J.N.A. Hooper *et al.*, 9.ii.1994. QM-G315107, Outer Gneerings, Sunshine Coast, 26°39.45'S, 153°12.90'E, 27.9 m, J.N.A. Hooper *et al.*, 15.x.1998. QM-G315659, Sunshine Reef, off Sunshine Coast, 26°24.77'S, 153°8.08'E, 27 m, S.D. Cook *et al.*, 11.x.1999. QM-G315764, North Halls, off Sunshine Coast, 26°20.77'S, 153°4.0'E, 21 m, S.D. Cook *et al.*, 13.x.1999. QM-G306244, S side Woody I., Hervey Bay, 25°20.07'S, 152°59.10'S, 3 m, J.N.A. Hooper *et al.*, 17.xi.1995. QM-G306288, Sponge Gardens, SW of Little Woody I., Hervey Bay, 25°20.02'S, 153°1.08'E, 19 m, J.N.A. Hooper *et al.*, 18.xi.1995. GREAT BARRIER REEF, QLD: QM-G307500, N side Polmaise Reef, Capricorn-Bunker Group, 23°33.05'S, 151°39.15'E, 12 m, J.N.A. Hooper *et al.*, 12.viii.1996. QM-G307750,

NE Point, Crab Spit, Low Isles, fore reef, 16°23.13'S, 145°34.05'E, 18 m, J.N.A. Hooper *et al.*, 16.i.1997. QM-G307862, SE tip of Wooded Islet, Low Isles, 16°23.13'S, 145°34.0'E, 16 m, J.N.A. Hooper *et al.*, 18.i.1997. QM-G314363, Curacao I. on west side, Palm Islands Group, 18°40.82'S, 146°32.62'E, 30 m, S.D. Cook *et al.*, 22.i.1999. QM-G314727, NE corner of Little Lindeman I., 20°25.32'S, 149°2.56'E, 22 m, S.D. Cook *et al.*, 2.vi.1999. QM-G314787, Cid Harbour, Whitsunday I., 20°16.82'S, 148°55.59'E, 18 m, S.D. Cook *et al.*, 2.vi.1999. QM-G314841, Alcyonarian Point, Hook I., Whitsunday Group, 20°3.93'S, 149°55.41'E, 15 m, S.D. Cook *et al.*, 3.vi.1999. QM-G314919, Cateran Bay, Border I., Whitsunday Group, 20°9.16'S, 149°2.54'E, 30 m, S.D. Cook *et al.*, 4.vi.1999. QM-G315420, Chauvel Reef, 20°49.54'S, 150°20.13'E, 19 m, S.D. Cook *et al.*, 7.vi.1999. QM-G317316, Double Rock, Elliott Heads, 24°53.88'S, 152°29.53'E, 7.8 m, S.D. Cook *et al.*, 11.x.2000, SCUBA. QM-G317381, NE of Bustard Head, 23°53.92'S, 151°50.53'E, 31 m, QDPI Fisheries, 8.x.2000, trawl. QM-G317988, NE of Gladstone, 23°41.73'S, 151°31.09'E, 25 m, QDPI Fisheries, Scallop Survey on FV 'Seadar Bay', 18.x.2001, trawl. QM-G318409, Pompey Reefs, 21°22.68'S, 151°14.88'E, 19.2 m, S.D. Cook *et al.*, 18.ii.2000. QM-G319404, NE of Gladstone, 23°39.06'S, 151°33.04'E, 29 m, QDPI Fisheries Scallop Survey on FV 'C-King', 18.x.2001, trawl. QM-G319430, E of Gladstone, 23°51.59'S, 151°41.39'E, 30 m, QDPI Fisheries Scallop Survey on FV 'C-King', 19.x.2001, trawl. QM-G320125, Man and Wife I., Keppel Islands, 23°7.08'S, 150°59.45'E, 17.4 m, J.N.A. Hooper *et al.*, 6.xi.2002. QM-G320208, Big Peninsula, Great Keppel I., 23°9.03'S, 150°58.4'E, 12 m, J.N.A. Hooper *et al.*, 7.xi.2002. QM-G320241, QDPI Scallop Survey 106 Shot 41, 22°45.68'S, 151°4.73'E, QDPI Fisheries Scallop Survey on FV 'Southern Intruder', 15.x.2002, trawl. QM-G320741, Mid Reef, Howick Group, 14°26.89'S, 144°52.88'E, 23 m, J.N.A. Hooper *et al.*, 3.vii.2003. QM-G320757, Houghton Reef, Howick Group, 14°31.19'S, 144°58.89'E, 20 m, J.N.A. Hooper *et al.*, 3.vii.2003. QM-G321570, Sykes Reef, Heron I, 23°27.07'S, 152°2.33'E, 19.2 m, S.D. Cook *et al.*, 8 m, 9.xi.2004. QM-G321700, eastern end, NorthWest I., 23°26.0'S, 151°36.49'E, 20.8 m, S.D. Cook *et al.*, 10.xi.2004. QM-G321765, Rock Cod Shoal, 23°40.62'S, 151°37.10'E, 14 m, S.D. Cook *et al.*, 11.xi.2004. QM-G321821, SW of Fitzroy I., 16°55.59'S, 145°59.29'E, 20 m, S.D. Cook *et al.*, 24.xi.2004. QM-G321858, Normanby I., N end of Frankland Is, 17°12.24'S, 146°4.45'E, 13 m, S.D. Cook *et al.*, 25.xi.2004. QM-G321913, Gibson Reef, 17°18.35'S, 146°20.65'E, 24 m, S.D. Cook *et al.*, 26.xi.2004. QM-G321955, Hall-Thompson Reef, 17°36.58'S, 146°26.51'E, 15 m, S.D. Cook *et al.*, 26.xi.2004. CORAL SEA TERRITORIES. QM-G320434, Melville Passage, Tydeman Reef, 13°59.37'S, 144°29.95'E, 32 m, J.N.A. Hooper *et al.*, 29.vi.2003. QM-G320648, Munro Reef, 14°18.15'S, 144°48.81'E, 23 m, J.N.A. Hooper *et al.*, 2.vii.2003. GULF OF CARPENTARIA, NT: QM-G300780, E of Gove Peninsula, 13°48.03'S, 136°21.04'E, 18.8 m,
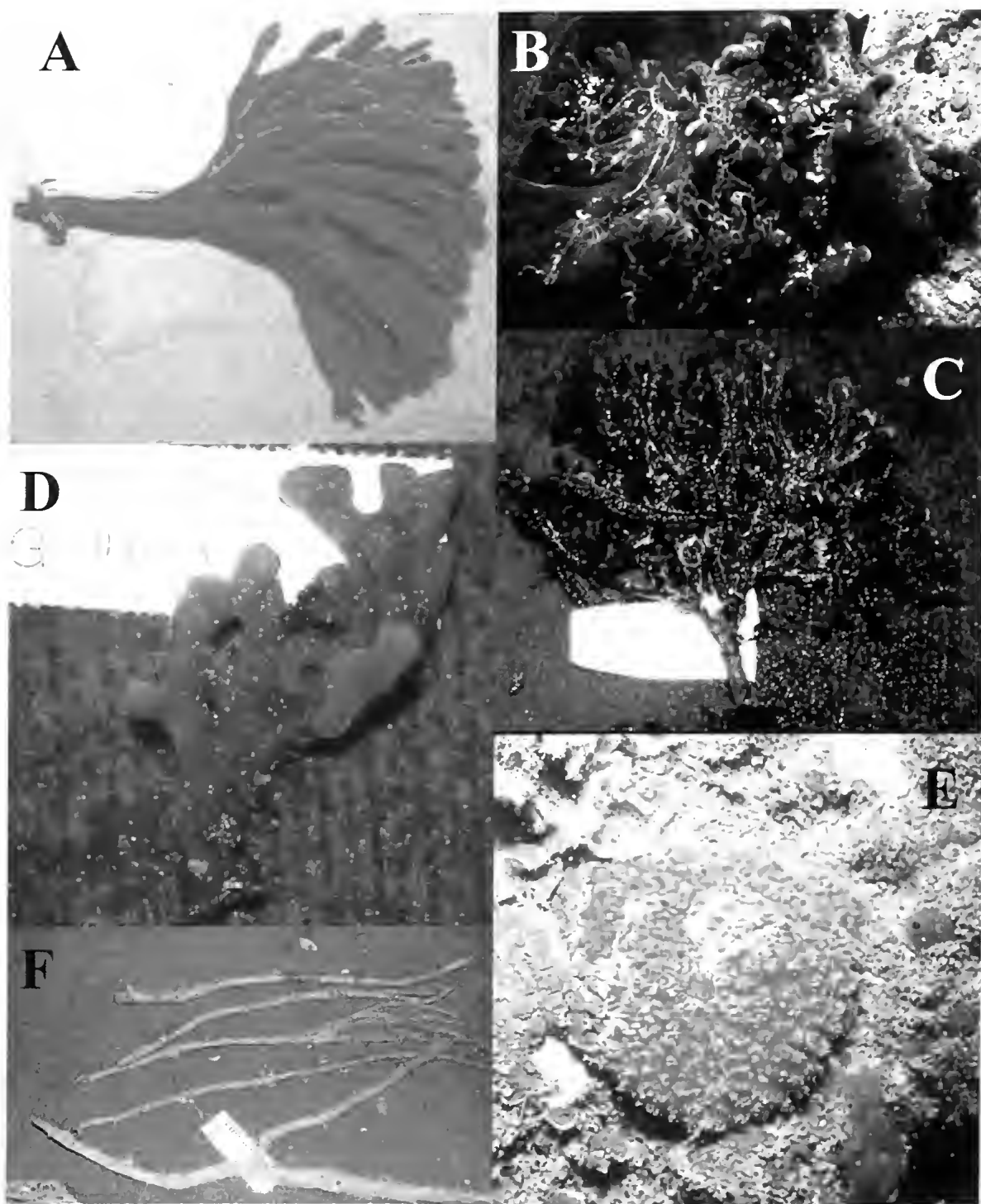
FIG. 8. Moreton Bay Raspailiidae fauna. **A**, *Raspailia (Raspailia) scorpa* sp. nov. (holotype, QM-G315208, on deck, from Moreton Bay). **B–C**, *Raspailia (Raspailia) kennedyi* sp. nov. (holotype, QM-G317177, alive and on deck, from Moreton Bay). **D**, *Raspailia (Raspaxilla) compressa* Bergquist (QM-G304878, on deck, from Mooloolaba). **E**, *Aulospongus similiaustralis* sp. nov. (QM-G303963, in situ, from Noosa). **F**, *Raspailia (Parasyringella) australiensis* Ridley (QM-G320811, on deck, Gulf of Carpentaria).
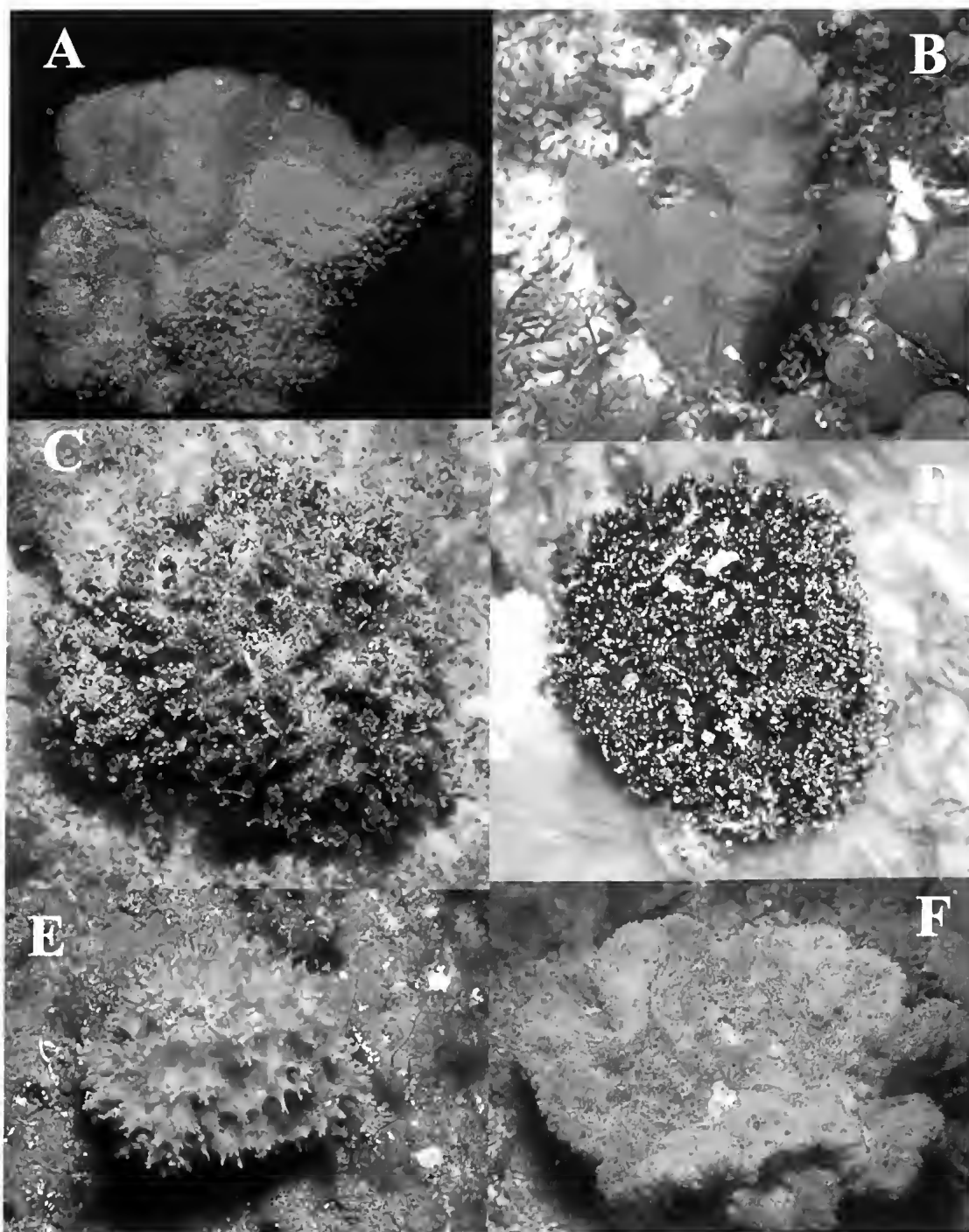
FIG. 9. Moreton Bay Raspailiidae fauna. **A**, *Sollasella moretonensis* Van Soest, Hooper, Beglinger & Erpenbeck (holotype, QM-G303227, in situ, from North Stradbroke I.). **B**, *Ceratopsis clavata* Thiele (specimen, QM-G301426, from Byron Bay). **C**, *Echinodictyum asperum* Ridley & Dendy (specimen, QM-G303197, in situ, from Moreton I.). **D**, *Echinodictyum conulosum* Kieschnick (specimen, QM-G317228, intertidal, from North Stradbroke I.). **E**, *Echinodictyum luteum* sp. nov. (paratype, QM-G306395, in situ, from Palau). **F**, *Echinodictyum mesenterinum* (Lamarck) (specimen, QM-G303959, in situ, Noosa).

S.D. Cook on CSIRO RV 'Southern Surveyor', 23.xi.1991, trawl. QM-G300792, E of Gove Peninsula, 12°37.02'S, 136°49.05'E, 26 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 23.xi.1991, dredge. QM-G300818, E of Groote Eylandt, 13°1.08'S, 136°43.0'E, 22 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 23.xi.1991, trawl. NORTHERN TERRITORY. QM-G303326, East Point Bommies, Darwin Harbour, 12°24.08'S, 130°48.13'E, 10 m, J.N.A. Hooper & L.J. Hobbs, 23.ix.1993. QM-G303429, Mandorah Jetty, Darwin Harbour, 12°26.1'S, 130°46.02'E, 9 m, J.N.A. Hooper & L.J. Hobbs, 25.ix.1993. QM-G313318, N of Bathurst I., Arafura Sea, 11°19.98'S, 130°12.18'E, 40 m, T. Wassenberg CSIRO, 10.iii.1997, trawl. QM-G314244, Arafura Sea, north of Cape Wessel, 10°45'S, 136°52.0'E, 53 m, S.P. Leys on CSIRO RV 'Southern Surveyor', 24.ix.1998, trawl. WESTERN AUSTRALIA. QM-G304585, Monkey Mia, Eastern Bluff, Peron Peninsula, Shark Bay, 25° 48'S, 113°45'E, subtidal, R. Smolker, Univ. Southern California, 21.vi.1994. QM-G306004, SW of Cape Jaubert, 19°27.13'S, 117°20.05'E, 86 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 31.viii.1995, trawl. QM-G306009, NE of Dampier, 19°34.08'S, 117°14.15'E, 74 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 31.viii.1995, trawl. QM-G306173, SW of Broome, 19°24.15'S, 118°3.03'E, 68 m, S.D. Cook on CSIRO RV 'Southern Surveyor', 6.ix.1995, trawl. NEW CALEDONIA. QM-G304705, Isle de Sable, 19°15'S, 163°48.0'E, 11 m, J. Vacelet, 25.iv.1989. SINGAPORE. QM-G313102, Pulau Tembakul (Kusu I.), Freyberg Channel, 1°13.08'N, 103°51.12'E, 18.7 m, J.N.A. Hooper & J.A. Kennedy, 2.v.1997. MALAYSIA. QM-G321087, SW peninsular, centre of bay W of T. Melano, 2°1.7'N, 109°39.2'E, 8 m, N.J. Pilcher, Marine Research Foundation, 30.v.2003. VIETNAM: QM-G300050, Off Han Rai I., Gulf of Thailand, 9°43.12'N, 104°20.10'E, 4 m, Y. Yakovlev on USSR RV 'Akademik Oparin', 29.x.1987. PHILIPPINES. QM-G304786, NW side Olango I., off Cebu, 10°16.05'N, 124°2.03'E, 23 m, Coral Reef Research Foundation, 8.ii.1994. Further material as listed in Hooper (1991).

Habitat and Distribution. Subtidal and shallow coastal rock, live and dead coral reefs, with a known bathymetric distribution from intertidal to 86 m depth. This species has a circum-Australian distribution, and also widely distributed throughout the Indo-west Pacific (see records also from Hooper 1991), and it is particularly common in tropical waters on both sides of the continent. The present study greatly expands the known distribution along the Great Barrier Reef down to Moreton Bay. The type locality is unknown other than 'Australian Seas', Peron and Lesueur collection (Fig. 6D).

Remarks. This species has been comprehensively redescribed by Hooper (1991), including its morphological variability across its extensive distribution, which from the present samples has expanded into the northwestern and southwestern Pacific. The species has a very characteristic growth form that has become aptly known as 'birds nest'. Sponges are typically erect, vasiform or cup-shaped, on a short stalk or attached to substratum directly. Live colouration is also fairly consistent and evenly pigmented dark purple or blue-purple throughout, varying only slightly depending on water depth and clarity. Texture is very harsh, only slightly compressible or flexible, and difficult to tear.

DISCUSSION

The present study increases the raspailiid fauna of the Moreton Bay region from three to eleven species including four new species; increases the known Australian fauna to 63 species; and significantly expands the known geographic ranges of many of these. Of the Moreton Bay species three are known only so far from this region and the southern Great Barrier Reef. Three other species extend into the northern tropical waters of the Northern Territory and/or Western Australian region, and five species have more extensive Indo-west Pacific distributions (Table 5). The occurrence of local (apparent) endemic species in the Moreton Bay region is well-known, with the region being a major biogeographic transition zone between the southern (Peronian) and northern (Solanderian) faunas. In addition to having a peculiar mix of both temperate and tropical species (e.g. Endean *et al.* 1956), the region is known to contain approximately 30 species of marine invertebrates found nowhere else, and which probably represent relics from once more widespread habitats, or still remain undetected in other enclaves along the coast (Davie & Hooper 1998). Most of the sponges studied here belong to the tropical fauna are at the southern-most point in their distributions. This number of apparent endemic species is likely to rise significantly with an increased taxonomic effort in this region, as demonstrated by the present discovery of new sponge species from what was thought to be a relatively well known fauna.

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New species of Raspailiidae (Porifera: Demospongiae: Poecilosclerida) from southeast Queensland

Hooper, J.N.A., Sutcliffe, P. & Schlacher-Hoenlinger, M.A.

Text to be added at the end of page 22 of *Memoirs of the Queensland Museum — Nature*, volume 54(1).

TABLE 1. Comparisons in the range (and mean) spicule measurements between *Raspailia (Raspailia) scorpa* sp. nov. and the allied *R. (R.) phakellopsis* Hooper 1991.

Material	Ectosomal styles	Choanosomal styles	Subectosomal styles	Echinating acanthostyles
R. (R.) scorpa sp. nov. (holotype QMG315208)	210-350 × 1-2 μm (315.8 × 1.9 μm)	290-460 × 10-11 μm (378.0 × 11.0 μm)	1000-1600 × 5-13 μm (1288.6 × 9.0 μm)	80-140 × 4-5 μm (125.8 × 4.9 μm)
R. (R.) phakellopsis (holotype NTM Z1950)	173-302 × 0.5-3 μm (231.0 × 1.5 μm)	311-465 × 9-8 μm (392.7 × 13.2 μm)	820-1835 × 8-17μm (1349.6 × 12.4 μm)	125-156 × 5-9 μm (133.2 × 7.1 μm)

TABLE 2. Range (and mean) of spicule measurements in *Raspailia (Raspailia) kennedyi* sp. nov.

Material	Choanosomal styles	Subectosomal styles	Ectosomal styles (anisoxeas)	Echinating acanthostyles
Holotype QMG317177	350-830 × 9-12 μm (497 × 8.53 μm)	900-1200 × 7-9 μm (1077 × 8.2 μm)	140-290 × 1-2 μm (203.50 × 1.66 μm)	50-70 × 4-6 μm (61.43 × 4.9 μm)

TABLE 3. Range (and mean) spicule measurements in specimens of *Aulospongus similiaustralis* sp. nov. and comparison with related species of *Aulospongus*.

Material	Choanosomal styles	Subectosomal tylostyles	Echinating acanthostyles
Holotype QMG300079	230-380 × 9-20 μm (300.3 × 10.8 μm)	690-1120 × 4-10 μm (925.6 × 9.7 μm)	70-255 × 2-8 m (97.9 × 4.4μm)
Paratypes QMG315526	150-350 × 8-20 μm (248.3 × 11.8 μm)	780-1260 × 10 μm (974.6 × 10 μm)	60-120 × 5-7μm (87.3 × 5.1μm)
QMG317317	210-435 × 10-20 μm (342.1 × 16.1 μm)	800-1200 × 6-11 μm (955.7 × 9.4 μm)	82-150 × 5-10μm (101.2 × 6.8μm)
QMG320085	180-370 × 6-20 μm (292.2 × 14.1 μm)	720-1110 × 6-10 μm (932.2 × 8.7 μm)	65-130 × 3-6μm (85.4 × 4.6μm)
Specimens QMG304007	150-340 × 12-20 μm	950-1300 × 8-15 μm	85-125 × 4-5 μm
QMG304879	240-370 × 10-20 μm	850-1050 × 10-15 μm	80-130 × 6-12 μm
QMG303963	190-345 × 15-20 μm	800-1100 × 5-10 μm	80-120 × 5- μm
QMG317276	310-430 × 18-20 μm	900-1250 × 5-10 μm	80-125 × 7-11 μm
QMG306292	270-440 × 8-25 μm	790 1200 × 4-11 μm	80-165 × 5-10 μm
QMG315777	280-400 × 4-10 μm	900-1410 × 6-15 μm	90-130 × 6-8 μm
QMG315732	270-370 × 9-18 μm	700-1400 × 5-15 μm	80-130 × 5-7 μm
QMG315610	175-390 × 7-20 μm	800-1350 × 4-16 μm	80-130- × 3-5μm
A. tubulatus (Bowerbank 1873) (data from Hooper *et al.* 1999)	304-462 × 16-24 μm	Absent (ectosomal styles: 212-250 × 2-3 μm)	109-126×5-10 μm

TABLE 4. Range (and mean) spicule measurements for specimens of *Echinodictyum luteum* sp. nov.

Material	Primary choanosomal oxeas	Secondary choanosomal oxeas	Echinating acanthostyles
QMG304769 holotype	205-440 × 5-11µm (269.8 × 7.37µm)	140-320 × 2-6µm (204.8 × 3.76µm)	90-135 × 4-7µm (117.6 × 4.84µm)
QMG317152 paratype	150-580 × 5-13µm (247.5 × 8.75µm)	110-425 × 1-7µm (223.8 × 3.96µm)	105-130 × 3-8µm (115.6 × 5.96µm)
QMG306395 paratype	200-500 × 4-11µm (287 × 6.12µm)	170-400 × 1-2µm (220.27 × 1.33µm)	120-180 × 4-8µm (141.48 × 5.6µm)

TABLE 5. Updated checklist of Raspailiidae recorded from Australian territorial waters (1, Dampierian Province, Geraldton (Western Australia) to Cape York (Queensland). 2, Solanderian Province, Cape York (Queensland) to Coffs Harbour (New South Wales). 3, Peronian Province, Coffs Harbour (New South Wales) to shallow coastal regions of northern Victoria and deeper waters off northeastern Tasmania. 4, Maugean Province, Bass Strait and shallow waters of Tasmania. 5, Flindersian Province, western Victoria to Geraldton (Western Australia). 6, Australian Antarctic and subantarctic Territories. Provinces after Bennett & Pope (1957). Data modified and updated from Hooper (1991).

Species	1	2	3	4	5	6	Other locality
Raspailia (Raspailia) atropurpurea (Carter, 1885)			×	×			
Raspailia (Raspailia) echinata Whitelegge, 1907			×				
Raspailia (Raspailia) kennedyi sp. nov.		×					
Raspailia (Raspailia) gracilis (Lendenfeld, 1888)			×				
Raspailia (Raspailia) phakellopsis Hooper, 1991	×						
Raspailia (Raspailia) pinnatifida (Carter, 1885)				×			
Raspailia (Raspailia) scorpa sp. nov.		×					
Raspailia (Raspailia) tenella (Lendenfeld, 1888)			×				
Raspailia (Raspailia) vestigifera Dendy, 1896	×			× ?			
Raspailia (Raspailia) wilkinsoni Hooper, 1991		×					New Caledonia, Vanuatu
Raspailia (Clathriodendron) arbuscula (Lendenfeld, 1888)	×		×				New Zealand
Raspailia (Clathriodendron) bifurcata Ridley, 1884	×	×	×				
Raspailia (Clathriodendron) cacticutis (Carter, 1885)				×			
Raspailia (Clathriodendron) darwinensis Hooper, 1991	×						
Raspailia (Clathriodendron) desmoxyiformis Hooper, 1991	×						
Raspailia (Clathriodendron) keriontria Hooper, 1991	×						
Raspailia (Clathriodendron) melanorhops Hooper, 1991	×						
Raspailia (Clathriodendron) paradoxa Hentschel, 1911					×		
Raspailia (Raspaxilla) compressa Bergquist, 1970	×	×			×		New Zealand
Raspailia (Raspaxilla) frondula (Whiteleggge, 1907)			×				
Raspailia (Raspaxilla) reticulata Hooper, 1991		×					
Raspailia (Raspaxilla) wardi Hooper, 1991	×						

TABLE 5. continued …

Species	1	2	3	4	5	6	Other locality
Raspailia (Parasyringella) australiensis Ridley, 1884	×	×					
Raspailia (Parasyringella) clathrata Ridley, 1884		×					
Raspailia (Parasyringella) elegans (Lendenfeld, 1887)	×						
Raspailia (Parasyringella) nuda Hentschel, 1911	×						
Raspailia (Parasyringella) stelliderma (Carter, 1885)				×			
Raspailia (Hymeraphiopsis) irregularis Hentschel, 1914						×	
Aulospongus similiaustralis sp. nov.		×					
Sollasella digitata Lendenfeld, 1888			×				
Sollasella moretonensis Van Soest, Hooper, Beglinger & Erpenbeck, 2006	×	×					
Ectyoplasia frondosa (Lendenfeld, 1887)	×		?				
Ectyoplasia tabula (Lamarck, 1814)	×				×		
Ectyoplasia vannus Hooper, 1991	×						
Endectyon elyakovi Hooper, 1991	×	×					
Endectyon fruticosum aruense (Hentschel, 1912)	×						Indonesia, Thailand
Endectyon thurstoni (Dendy, 1887)	×						E coast India
Endectyon xerampelina (Lamarck, 1932)							Unknown, possibly Australia
Trikentrion flabelliforme Carter, 1882	×				?		Indonesia, PNG
Cyamon aruense Hentschel, 1912	×						Indonesia
Eurypon graphidiophorum Hentschel, 1911					×		
Amphinomia sulphurea Hooper, 1991	×						
Ceratopsion dichotomum (Whitelegge, 1907)			×				
Ceratopsion axiferum (Hentschel, 1912)	×						Indonesia
Ceratopsion clavatum Thiele, 1898		×					Japan, New Caledonia, Papua New Guinea
Ceratopsion montebelloense Hooper, 1991	×						
Ceratopsion palmatum Hooper, 1991	×						New Caledonia
Thrinacophora cervicornis Ridley & Dendy, 1886	×						Indonesia, Philippines
Axechina raspailioides Hentschel, 1912	×						Indonesia
Echinodictyum arenosum Dendy, 1896				×			
Echinodictyum asperum Ridley & Dendy, 1886	×	×					Indo-Pacific, Tahiti to Gulf of Manaar, Chuuk to northern Australia
Echinodictyum austrinus Hooper, 1991					×		
Echinodictyum cancellatum (Lamarck, 1814)	×	×					Indonesia
Echinodictyum carnioides (Lamarck, 1814		×					Indonesia
Echinodictyum clathrioides Hentschel, 1911	×				×		
Echinodictyum connulosum Kieschnick, 1900	×	×					
Echinodictyum costiferum Ridley, 1884		×					

TABLE 5. continued …

Species	1	2	3	4	5	6	Other locality
Echinodictyum fruticosum Hentschel, 1911	×						
Echinodictyum lacunosum Kieschnick, 1898		×					
Echinodictyum luteum sp. nov.		×					Palau
Echinodictyum mesenterinum (Lamarck, 1814)	×	×	×	×	×		Indo-west Pacific: Philippines, New Caledonia, Singapore, Malaysia, Vietnam
Echinodictyum nidulus Hentschel, 1911	×				×		
Echinodictyum rugosum Ridley & Dendy, 1886	×						Indonesia

Morbakka fenneri, a new genus and species of Irukandji jellyfish (Cnidaria: Cubozoa)

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ABSTRACT

A cubozoan jellyfish, *Morbakka fenneri* gen. nov., sp. nov. is described. *Morbakka* differs from other genera and species in the Carybdeida by having a large, warty body; flat, ribbon-shaped tentacles; a prominent upward-pointing 'thorn' at the bend of the pedalial canal, and conspicuous broadening of the canal where it meets the tentacle; frown-shaped or dumbbell-shaped rhopalial niche ostium; long, straight, rabbit-ear shaped rhopalial horns; lack of non-lensed eye spots on the rhopalia; and three types of tentacular nematocysts and two types of bell nematocysts. Its morphology, genetics and sting symptoms clearly put it in the Irukandji group (i.e., *Carukia*, *Malo*, *Gerongia*), most closely related to *Gerongia rifkinae*. A larger northern Queensland form, and a smaller New South Wales form of *Morbakka* may also prove to be specifically distinct. *Morbakka* has been associated with severe Irukandji syndrome. ❑ *Cnidaria, Cubozoa, Tamoyidae, Irukandji syndrome, fire jelly, jellyfish, marine stingers, Queensland, Australia.*

A large and conspicuous eastern Australian cubozoan commonly called 'morbakka', 'fire jelly' or 'tamoya', has been well known to marine scientists, and to Queensland Surf Life Savers, for more than 20 years. Curiously it has never been properly classified or formally described, and this is finally undertaken in the present paper.

Morbakka was first described in the non-taxonomic sense by Southcott (1985), and has been extensively discussed by Fenner (1985, 1986b), Williamson *et al.* (1996), and others (see literature compilation under genus Remarks). However, more than 20 years later, our knowledge of this conspicuous and important animal has progressed little. Fenner (1986b, 1991, 1997) demonstrated that it can give systemic symptoms similar to Irukandji syndrome, and Little *et al.* (2006) recently implicated it (as 'fire jelly') in a serious sting resulting in heart failure. However, its reproductive biology, predator-prey ecology, and seasonal patterns have never been investigated, and nor have its toxins been studied.

Hopefully, the first formal description of the genus that is presented here, and the summary of current knowledge included, will help to stimulate further taxonomic investigation, as well as essential research into ecology, toxinology, and basic biology.

MATERIALS AND METHODS

All taxonomic observations and measurements were made on preserved material unless otherwise noted. Measurements were made with Max-Cal digital calipers to the nearest 0.01 mm. Bell height (BH) was measured from the apex of the bell to the velarial turnover. Diagonal bell width (DBW) was measured across diagonal pedalia on a flattened specimen, at the height where the pedalium joins the exumbrella of the bell. Interrhopalial width (IRW) was measured between adjacent rhopalia, with the specimen flattened. Tentacle base width (TBW) was measured at the uppermost part of the tentacle, immediately below the pedalium; if the tentacle was flattened, width was measured across the widest points. In opaque specimens, a search

for phacellae was made by making a small incision in the upper corners of the bell, and then pulling back a small amount of mesoglea to expose the floor of the stomach, or by opening up the full length of the body wall to expose the stomach, and then opening the stomach in the same manner. In transparent specimens, absence of phacellae was obvious. Nematocysts were examined and measured with a Leica DMLB compound microscope and Leica IM-50 Image Manager v. 1.20 for Windows; all observations and photographs were made through a 40x objective (i.e., 400 x magnification). Nematocysts were identified following the keys of Calder (1974), Mariscal (1971), Williamson *et al.* (1996), and Gershwin (2006a).

Abbreviations used. Australian Museum, Sydney (AM); Museum of Tropical Queensland, Townsville (MTQ); Queensland Museum, Brisbane (QM); and South Australian Museum, Adelaide (SAM). Specimens from the Peter J. Fenner international cubozoan collection are indicated with his initials (PJF), and are housed in the Queensland Museum; specimens from the Ronald V. Southcott collection are indicated with his initials (RVS) and correspond to extensive notes archived in the South Australian Museum. Everywhere in the text that 'morbakka' is not italicised, it is being used as a common name.

SYSTEMATIC ACCOUNT
Phylum CNIDARIA Verrill, 1865
Subphylum MEDUSOZOA Petersen, 1979
Class CUBOZOA Werner, 1973
Order CARYBDEIDA Gegenbaur, 1856
(sensu Werner, 1984)
Family TAMOYIDAE Haeckel, 1880
(sensu Gershwin, 2005a)

Morbakka gen. nov.
Diagnosis. Tamoyidae with tall, robust, conspicuously warty body; with flat, broad, ribbon-like tentacles; with well developed 'spike' in bend of pedalial canal; with conspicuous perradial lappets on the velarium; with long, straight 'rabbit-ear-form' rhopalial horns; exumbrellar warts typically coloured bright pink.

Type species. *Morbakka fenneri* sp. nov., here designated.

Etymology. The genus name, *Morbakka*, is taken from the common name 'Morbakka', which was derived by Southcott (1985) from 'Moreton Bay carybdeid'. Using the same term for both the scientific and common name should prevent any confusion in future reference to these animals. Gender is masculine.

Remarks. Gershwin (2005a, and earlier papers) considered Morbakka to be so closely allied to the 'Darwin carybdeid', *Gerongia rifkinae* Gershwin & Alderslade, 2005, that she considered them to belong to the same genus. However, the cnidomes are so distinct, as are fine structures such as the rhopalial horns and velarial canals, that I now believe generic distinction is necessary. Nevertheless *Gerongia* and *Morbakka* form a clade distinct from the 'true Irukandjis' (*Carukia* species), as well as from the 'pseudo-Irukandjis' (*Malo* species). Sting data indicate that *Malo* spp. are the most dangerous because they can cause life-threatening hypertension. Species of *Carukia* cause distressing, but not life-threatening illness, while the *Gerongia* + *Morbakka* clade cause the least severe envenomations and may be termed 'mild Irukandjis'. It should be noted that symptoms resembling Irukandji-syndrome can also result from stings from the multi-tentacled form of *Physalia* (Hydrozoa: Siphonophora), *Gonionemus* (Hydrozoa: Limnomedusae), *Nemopilema nomurai* (Scyphozoa: Rhizostomeae), as well as at least two cubozoans in the family Alatinidae (Fenner *et al.* 1993; Williamson *et al.* 1996; Yoshimoto & Yanagihara 2002; Gershwin 2005a, 2005c).

Locally, *Morbakka* has often, and erroneously, been identified as *Tamoya*, however *Morbakka* lacks any trace of the gastric phacellae that are diagnostically present and vertical in *Tamoya*.

Previous literature relating to *Morbakka*.

Specific to Moreton Bay form. As Morbakka — Southcott 1985: 324 (derivation of name); Fenner *et al.* 1985: 550–555 (severe sting case at Moreton Bay, sting experiments with specimens from Mackay); Fenner 1987: 97, fig. 3 (sting at Maroochydore, Sunshine Coast); Fenner 1997: 36–39, 51, 102-104, and throughout (stings and specimens, Sydney to Mackay). As *Tamoya virulenta* — Davie 1998: 238 (field guide). As *Tamoya gargantua* — Payne 1960: 5 (Moreton Bay and Gold Coast).

Specific to larger northern form(s). As Morbakka — Fenner *et al.* 1985: 550–555 (severe sting case
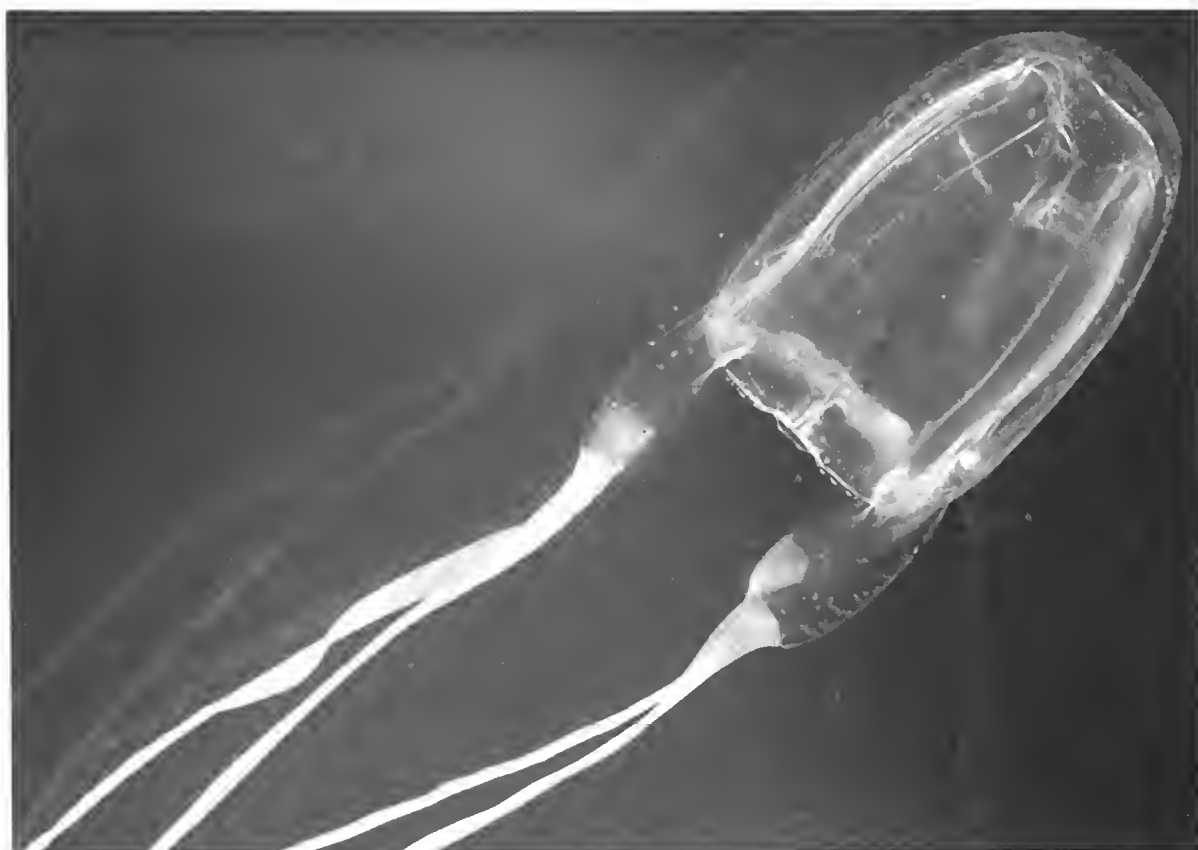
FIG. 1. *Morbakka fenneri* sp. nov., holotype specimen (QM-G322299), from Moreton Bay, photographed live (photo copyright Queensland Museum, used with permission).

at Moreton Bay, sting experiments with specimens from Mackay); Fenner 1986b: 118–119 (fire jelly, identification, stings; Mackay); Fenner 1997: 36–39, 51, 102–104, and throughout (stings and specimens, Sydney to Mackay); Gershwin 2006a: 11, 41, pl. 23 (cnidome). As Fire jelly — Little *et al.* 2006: 426, table (life-threatening envenomation, Briggs Reef, off Cairns Qld).

Non-specific mention. As Morbakka — Fenner 1986a: 99 (fire jelly, stings); Burnett & Calton 1987: 581–602 (toxicology); Williamson *et al.* 1987: 222–223 (identification, stings, treatment); Fenner 1991: 638–639 (fire jelly, morbakka comprises two species at least); Gurry 1992: 31 (medical); Franc 1995: 914 (stings); Pearn 1995: 107 (stinging); Williamson & Burnett 1995: 105 (fire jelly, medical); Holmes 1996: S26 (stings); Williamson *et al.* 1996: 148–149, 241–245, and various, pl. 9.7 (medical and biological); Morandini & Marques 1997: 188–189 (comparison with Brazilian syndrome); Fenner 1998: 22–27 (fire

jelly, Irukandji-like syndrome); White *et al.* 1998: 113–114 (medical); Sutherland & Nolch 2000: 17–18 (fire jelly, medical); Burke 2002: 19 (stings); Taylor *et al.* 2002: 175–180 (comparison to Irukandji sting of unknown origin); Gershwin 2005a: 118, pl. 4.6B, D, and throughout (taxonomy and phylogeny); Gershwin 2005b: 23 (comparison with *Malo maxima* and other Irukandjis); Gershwin 2005c: table 1 (comparison with other carybdeid forms); Gershwin & Alderslade 2005: 27–36 (comparison to *Gerongia rifkinae*); Gershwin 2006b: 801–802 (reply to Little *et al.* 2006 paper, comments on priority of claims in authorship of knowledge); Fenner 2006: 802–803 (reply to Little *et al.* 2006 paper); Gershwin 2007: 64–66 (comparison with other Irukandji species. As Tamoya — ? Pope 1951: 270–272 (New Caledonia, harvested for food); Exton *et al.* 1989: 625–626 (fire jelly, use of cold packs); Sutherland 2001: 607–609 (medical); Fenner 2002: 1169 ('Irukandji-like' syndrome).

Morbakka fenneri sp. nov.
(Figs 1–5)

Tamoya virulenta — Davie, 1998: 238, colour photograph [reproduced here as Fig. 1] (not *T. virulenta* Kishinouye, 1910).

Tamoya gargantua — Payne, 1960: 5; Moreton Bay and Gold Coast. (not *T. gargantua* Haeckel, 1880).

Material examined. HOLOTYPE. QM-G322299, North Stradbroke I., 13.01.1998, coll. Dept. of Environment; 110.41 mm BH, 98.84 mm DBW, 50.90 mm IRW, 16.49 mm TBW (Figs. 1, 2A).

PARATYPES. **Queensland**: QM-G313646, Scarborough Boat Harbour, coll. Scarborough Seafoods, 30.01.1998. QM-G317014 [PJF coll.], no locality, coll. Australian Institute of Marine Science. QM-G317016 [PJF coll.], Cape Hillsborough, N. of Mackay, D. Barker, 9.05.1987. QM-G317017 [PJF coll.], Bowen Harbour, Bowen, 20.05.1989. QM-G317018 [PJF coll.], Slade Point, N. of Mackay, D. Barker, 29.04.1989. QM-G317019 [PJF coll.], Slade Point, N. of Mackay, D. Barker, 29.04.1989. QM-G317020 [PJF coll.], Eimeo Beach, N. Mackay, 30.10.1985. QM-G317022 [PJF coll.], no locality, coll. Australian Institute of Marine Science. QM-G317026 [PJF coll.], Mackay Harbour, no date. QM-G317028 [PJF coll.], Mackay Harbour Beach, P. Fenner, no date. QM-G317029 [PJF coll.], Ayr, M. Mulcahy, 1991. QM-G317030 [PJF coll.], Mackay Harbour, 19.01.1986. QM-G317031 [PJF coll.], no locality, coll. Australian Institute of Marine Science. QM-G317048 [PJF coll.], Cape Hillsborough, N. of Mackay, 9.05.1987. QM-G317049 [PJF coll.], Ayr, M. Mulcahy, no date. QM-G317063 [PJF coll.], Mackay, no date. QM-G317071, female specimen, off Townsville, coll. R. Hartwick (Stn CF3), Tucker trawl, 10.04.1981. MTQ-G61430, 1 large specimen with two large fish protruding from gut, locality unknown (from JCU teaching collection). SAM-H1598 [RVS A265], 1 dissected specimen, with shrimp high up under bell, off Sandgate, Moreton Bay, inshore water, near surface, coll. Zool. Dept. Univ. Qld, 10.01.1957. SAM-H1599, commercial fishing grounds off Sarina, S. of Mackay, R. and R. Marriage, 30.04.2005; tissues preserved in EtOH housed at SAM. SAM-H1600, Marina Mirage, Dickson Inlet, Port Douglas, coll. Brett Kilpatrick, 17.04.2003, forwarded by R. Hore. SAM-H1601, Balgal Beach, north of Townsville, coll. Balgal Beach police officers, 12.10.2004. SAM-H1612 [RVS A2831], Mackay Harbour, P. Fenner, 18.04.1985, at surface. SAM-H1613, Mackay, no data. SAM-H1614, 3 specimens [rehydrated after being dried], Mackay, 1980–90s. **New South Wales**: AM-G15791, Port Jackson, coll. Sydney University Zoology Dept.; 1 spec., c. 65 mm BH, 55 mm DBW. AM-G14529, Ramsgate Beach, Botany Bay, M. Logan, 15.05.1974; 37.17 mm BH, 34.2 mm DBW, produced severe sting.

Description of holotype. Bell 110 mm tall, half as wide, with evenly thick mesoglea of rigid consistency; with straight sides and flat to shallowly-rounded top. Exumbrellar surface with numerous gelatinous warts, especially concentrated apically; coronal furrow absent. Interradial furrows deep and well marked, extending to just above point of subumbrellar lamellae. Adradial furrows deep in lower half, with well defined interradial pillars and perradial 'smile lines'; shallower in upper half.

Pedalia 4, one on each corner of bell, simple and unbranched, long scalpel-shaped, lacking any overhang of inner keel (Fig. 2B). Pedalial canals quadratic in cross section throughout length, broadly flaring to meet tentacle; with strongly defined upward-pointing 'spike' at bend, adaxially along lamella, with rounded abaxium and point (Figs. 2B, C). Pedalia armed with haphazardly arranged, raised, horizontal bars of nematocysts confined to outer keel. Measurements of one pedalium: 53.70 mm in length, 23.82 mm in width at midpoint; at midpoint, pedalial canal 8.22 mm wide, inner keel 8.45 mm wide, and outer keel 7.56 mm wide; thus, ratio of the keels to the canal about 1:1:1. Tentacles 4, one per pedalium, unbranched; flat, ribbon-like, broad, with base considerably flared to meet pedalium.

Rhopalial niche region prominently raised upon 'perradial pillar' defined by adradial furrows on both sides. Rhopalial niche ostium with two covering scales (1 upper, 1 lower), both broadly convex in outline, forming frown-shaped or dumbbell-shaped ostium (Figs. 2D, E). Rhopalial horns could not be observed in this specimen due to partial opacity of preserved mesoglea, but observed in other specimens to be long, straight, with a 'rabbit ear' appearance (Figs. 2D, 3A). Subumbrellar rhopalial windows flat, indented only at point of rhopalial stalk (Fig. 3A); frenulum extending over window to point of rhopalial connection. Eye spots faded in this specimen by the time of study, but observed in other live specimens to lack lateral eye spots, similar to those described for *Malo maxima* and *Malo kingi* (Gershwin 2005b, 2007). Rhopalial warts not studied in this specimen, but observed on adaxial side of stalk in other specimens (Fig. 3B). Statolith shape unknown.

Velarium broad and heavy, connected to subumbrella with 4 perradial bracket-like frenulae.
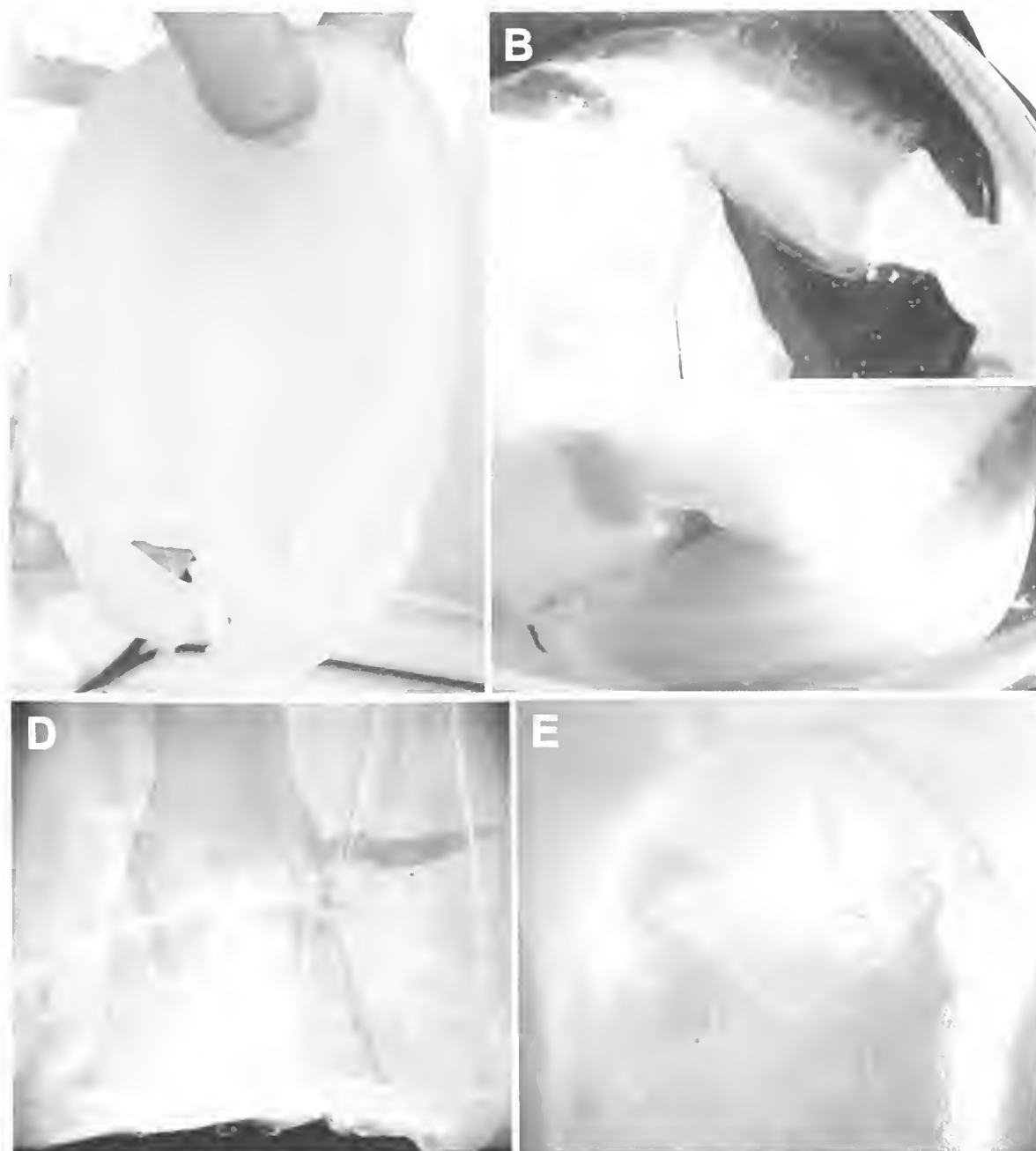
FIG. 2. *Morbakka fenneri*, sp. nov. **A**, holotype, preserved. **B**, paratype SAM-H1600 (Port Douglas), showing general pedalial shape, and form of pedalial canal. **C**, holotype, showing rounded tip of pedalial canal spike. **D**, paratype SAM-H1598 [RVS A265], showing general shape of rhopalial niche, upper and lower covering scales, and rhopalial horns. **E**, holotype, showing elevated rhopalial region.

Frenulae well developed, hollow along free edge, upon a solid gelatinous base; extending out onto velarium about halfway to margin, and in the other direction to top of rhopaliar windows as described above. Velarial canals so overgrown in this specimen so as to appear as one solid mass, with only the tips defined along the velarial margin; in most *Morbakka* specimens,
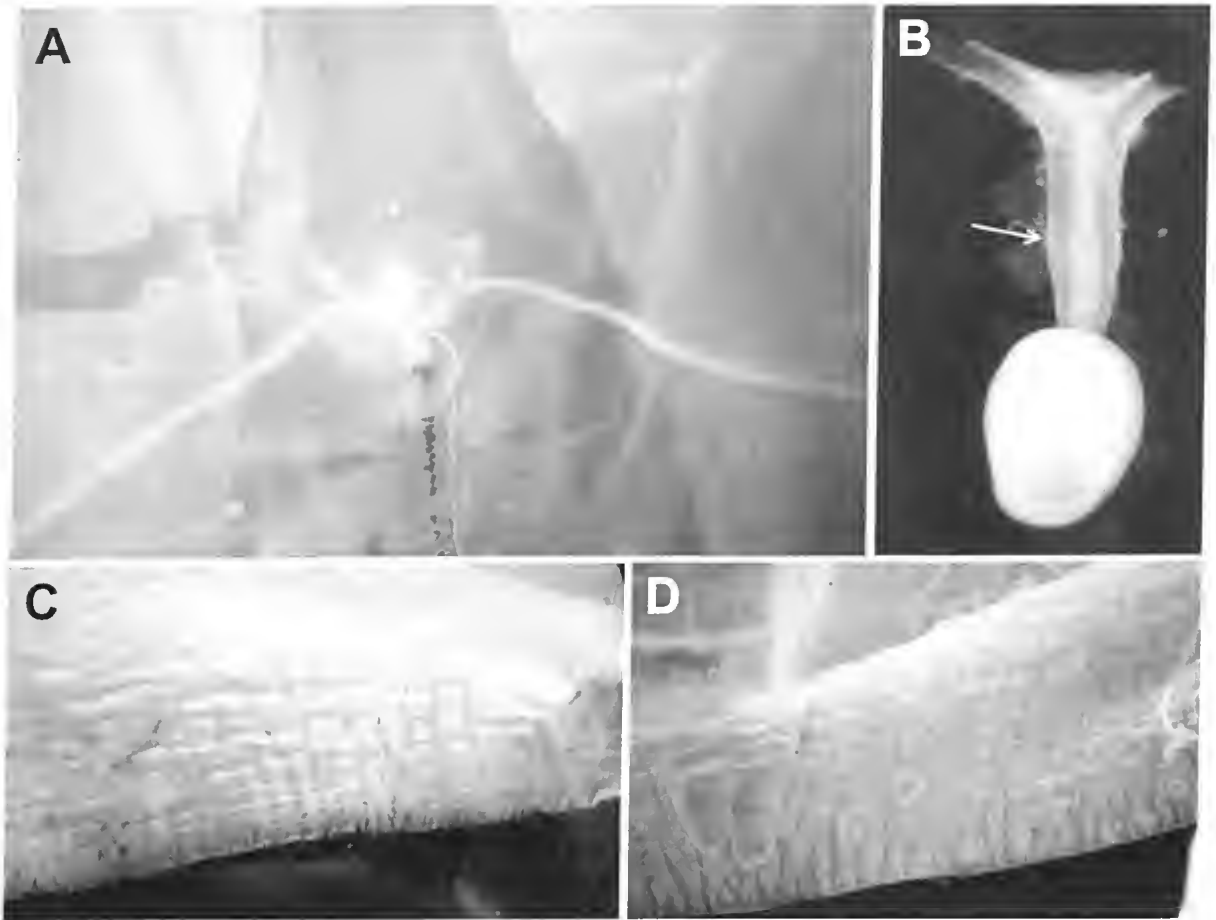
FIG. 3. *Morbakka fenneri* sp. nov. **A**, paratype SAM-H1598 [RVS A265], subumbrellar view of rhopaliar window and rhopaliar horns; note also upper portion of frenulum extending from rhopalium to bottom of photo. **B**, paratype SAM-H1598 [RVS A265], rhopalium dissected out of specimen, showing rhopaliar wart on stem (arrow). **C**, velarium; note lack of warts and massive perradial lappet just visible on left of photo. **D**, velarium, paratype specimen SAM-H1600 from Port Douglas; note narrow perradial lappets to left of photo, and gelatinous warts scattered over canals. Note also, different branching patterns between two specimens, parallel in C, dendritic in D.

velarial canals appear as separated, parallel, well-defined straight canals with numerous lateral diverticula, resembling 'feathers' or 'trees' (Fig. 3C), or as dendritic canals (Fig. 3D). Perradial lappets very narrowly triangular in shape in holotype (cf. Fig. 3D); in some specimens perradial lappets massive (Fig. 3C). Velarium armed with nematocyst warts scattered on lappets, lacking on canals; some other specimens lack warts (Fig. 3C) or warts lacking on lappets but present over canals (Fig. 3D).

Manubrium moderately long, extending to about one-half height of bell cavity. Mouth with four well-developed triangular lips, with slightly thickened margins and straight, uncrenulated edges (Fig. 4A). Stomach large and bag-like, connected to subumbrellar surface with well-developed mesenteries. Mesenteries flap-like in upper half of bell, with a fine cord extending down to rhopalium. Floor of stomach densely patterned with parallel corrugations (Fig. 4B; termed 'area corrugata' by Southcott, 1967); gastric phacellae lacking.

Gonads leaf-like, pleated, attached along each of 4 interradial septa as pairs of hemi-gonads; full-length of subumbrellar cavity, reaching both stomach and pedalial regions, with attachment along total length of gonadal sheets; gonads
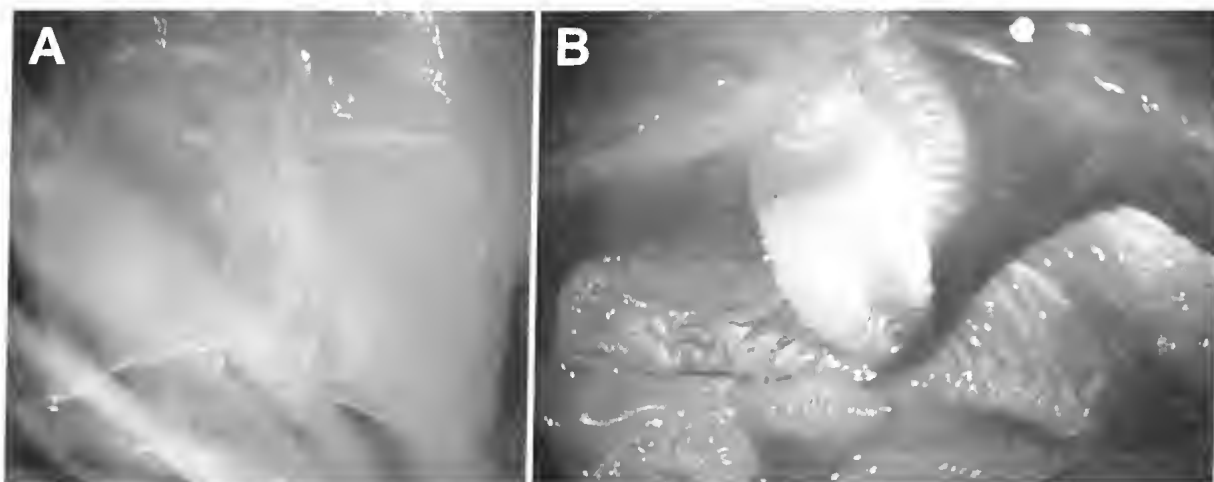
FIG. 4. *Morbakka fenneri* sp. nov. **A**, paratype SAM-H1600 from Port Douglas, manubrium and lips; note smooth, straight edges. **B**, paratype QM-G317071, area corrugata in stomach; note lack of gastric phacellae.

narrow in this specimen, about as broad as pillars, possibly immature or recently spawned. Inter-radial suture not interpreted due to thickness of mesoglea obscuring view.

Colouration: Preserved specimen with trans-lucent mesoglea; colourless warts; tentacles pink. In life (based on observations of other speci-mens), bell is transparent to translucent, nem-atocyst warts bright pink, and tentacles pale pink.

Nematocysts (Fig. 5). According to Cleland & Southcott (1965: pl. 2), the tentacles contain holo-trichous isorhizas and unidentified haplonemes. According to Hartwick (unpublished nematocyst identification poster), the tentacles contain micro-basic *p*-mastigophores, 45–75 μm long, and 2 types of football shaped isorhizas, 45 μm long, and the bell warts contain subspherical isorhizas of two types, similar to those on the tentacles. According to Gershwin (2006a), who studied the cnidome of a specimen from Port Douglas, the tentacles contain three types of nematocysts — club-shaped microbasic *p*-mastigo-phores (Type 4), spines scattered, 60–70 μm long x 13–18 μm wide; and two types of large oval isorhizas, one with loose tubule, one with tight tubule, 49–56 μm long x 28–34 μm wide. She further found that the bell warts contain two types of nematocysts: 1) spherical isorhizas, 27–30 μm long; and 2) oval, poorly defined, with papillated outer surface and loosely wound tubule, as wide as type 1, but 1.5 times as long.

Currently no information is available about the nematocysts of the manubrium.

Etymology. This species is named to honour Professor Peter Fenner AM, M.D., who has devoted much time and personal interest to resolving the differences between this species and other large cubozoans. I have unwavering admiration and respect for his knowledge and dedication to marine stinger research and stinger safety, and he has been a personal inspiration and mentor in my study of cubozoans.

Ecology. *Morbakka fenneri* is relatively rare, being only occasionally found, and then as solitary collections. No information presently exists as to its general behaviour, life cycle, or predator-prey relationships.

Distribution. *Morbakka fenneri* was first found in the Moreton Bay region; it is said to be com-monest at Redcliffe, but has also been found at Stradbroke Island. The larger form is most com-mon at Mackay, where one or two specimens a year are collected (P. and D. Barker, pers. comm.); a few specimens have been collected at Port Douglas or Cairns (B. Cropp, pers. comm.; R. Hore, pers. comm.); a single specimen was collected at Balgal Beach, north of Townsville, and a couple at Ayr, south of Townsville. It has also been collected offshore from Cairns (Little *et al.* 2006). A smaller form is occasionally found in New South Wales from Coffs Harbour to Sydney.

Sting Potential and Management. *Morbakka fenneri* is capable of inflicting a severe sting which may

FIG. 5. *Morbakka fenneri* sp. nov., tentacular nematocysts, from paratype specimen SAM-H1600 (Port Douglas). **A**, club-shaped microbasic p-mastigophores (with fibrils still connected to the nematocyst in the lower right). **B**, mastigophores and large oval isorhiza. **C**, mastigophore and large oval isorhiza. **D**, large oval isorhiza. [Previously published in Gershwin 2006a].

include symptoms similar to Irukandji Syndrome as first noted and described by Fenner *et al.* (1985) and Fenner (1991, 1997, 2006). Little *et al.* (2006) even reported a life threatening case, in which heart damage occurred, though this is exceptional.

Morbakka stings are best avoided by the use of protective clothing. Management of stings should include dousing the stung area with plenty of vinegar to neutralise undischarged nematocysts; ice packs may help to reduce pain and swelling, but should not be used prior to vinegar. If systemic symptoms onset (e.g., body pain, nausea or vomiting, difficulty breathing, sweating), or if in doubt, ring '000' for an ambulance; the patient should be transported to hospital as soon as possible.

Remarks. *Morbakka* is often erroneously called 'tamoya' among Queensland Surf Life Saving groups, but *Morbakka fenneri* and *Tamoya haplonema* (also sometimes locally called *Tamoya virulenta*) appear to be only convergently similar. No member of the Irukandji group in Australia, including *Morbakka*, possesses gastric phacellae, whereas the western Atlantic *Tamoya haplonema* does. Other differences between *Morbakka* and *Tamoya* include: *Morbakka* has well developed perradial lappets, whereas they are lacking in *Tamoya; Tamoya* has lateral eye spots, whereas *Morbakka* does not; and *Morbakka*, like the other species in the Irukandji group (i.e., *Carukia, Malo, Gerongia*), has pronounced rhopaliar horns, whereas they are absent in *Tamoya*. Furthermore, the nematocysts are entirely different:

Morbakka tentacles have three types of nematocysts, club-shaped microbasic *p*-mastigophores with dense spines the entire shaft length, and loose- and tight-tubule large oval isorhizas, whereas *Tamoya* tentacles have only one type of nematocysts, club-shaped rhopaloids with a very long shaft and spines concentrated on a swelling at the distal end, with a tuft of spines midway. *Morbakka* is also often colloquially called 'fire jelly', in reference to the pain of the sting; however, the common name 'fire jelly' is also often applied to any sting of unknown origin in tropical Queensland, so one must be cautious in interpreting sting data relating to these terms.

From its closest known genetic and morphological relative, *Gerongia rifkinae*, *Morbakka* is easily distinguished by its size and shape, bell wartiness, colouration of the warts, and nematocysts. Whereas *G. rifkinae* reaches about 60 mm BH and 20 mm BD, *Morbakka* come in at least two sizes: the classic Moreton Bay form reaches about 90 mm BH and 30 mm wide, and the northern form reaches about 180 mm BH and 60 mm wide; another much smaller form, about 25 mm BH and 10 mm wide, is known only from New South Wales. The bell of *G. rifkinae* is sparsely freckled with low purple nematocyst warts, whereas the bell of *Morbakka* is densely warted with magenta raised gelatinous knobs. Finally, the tentacular nematocysts of *G. rifkinae* are entirely Type 4 microbasic *p*-mastigophores, whereas three types of nematocysts are present on the tentacles of *Morbakka*, as described above. A comparative table of diagnostic characters of genera in the Tamoyidae was given by Gershwin & Alderslade (2005).

Fenner (1986b, 1991, 1997) was the first to note consistent differences between typical Moreton Bay and north Queensland forms, suggesting that 'morbakka' comprises at least two different species. North Queensland morbakkas are typically large, however large specimens do also occur in Moreton Bay that closely resemble the northern form. Thus, the taxonomic and geographical boundaries remain problematic. Furthermore, there is a small New South Wales form that appears to be genuinely rare, and is currently only known from a small number of photographs and poorly preserved specimens. So, while there is some evidence for three (or more) potential *Morbakka* species, only *M. fenneri* is currently here recognised. Resolution of this issue will require a more detailed study of morphology, and internal structures, of a good series of specimens from each of the three groups — perhaps reinforced by additional molecular analyses.

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Sea anemones (Cnidaria: Anthozoa: Actiniaria) of Moreton Bay

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ABSTRACT

Nineteen species of sea anemones se*nsu stricto* (Anthozoa: Zoantharia: Actiniaria) are documented from the Moreton Bay region in eastern Australia, based primarily on specimens observed and collected during the Moreton Bay International Marine Biological Workshop in February 2005. Each species is taxonomically diagnosed, and information on the distribution of these species elsewhere in Australia is provided based on new field observations and museum records. Three species (*Anthopleura handi*, *A. buddemeieri* and *Verrillactis paguri*) were not previously recorded from Australia. *Actinia australiensis* was previously known only from south of Moreton Bay, and *Gyractis sesere* was recorded from eastern Australia for the first time. An unidentified species of *Diadumene* was found, providing the first record of the genus from Australia. A key to the 18 fully identified species is included. The sea anemone fauna reported in this paper is predominantly tropical to subtropical, with 14 species known primarily from the tropics, and four known primarily from the temperate zone; the other was not identified to species. ❏ *Australia, biogeography, new records, taxonomy.*

The Moreton Bay International Marine Biological Workshop, held in February 2005, provided us an opportunity to study species composition and distribution of sea anemones (cnidarian order Actiniaria) within and adjacent to Moreton Bay. We review the fauna from this region, and provide an account of 19 species, based mainly on external features of live animals, and update Australian distribution records for those species. A key that can be used to identify the 18 fully identified species in life is included.

This subtropical location in southeast Queensland has a marine biota with both temperate and tropical elements, including corals and associated coral reef organisms (Tibbetts *et al.* 1998; Dennison & Abal 1999). The environment is influenced by outflows from several rivers, and proximity to Greater Brisbane, a large and rapidly growing city. The offshore region is still relatively pristine and is affected by the tropical East Australian Current, as well as intermittent northerly flowing currents. Rainfall is variable in the region, typically being high during the summer months (December to February). Episodic freshwater flooding may profoundly influence the fauna of inner Moreton Bay: such events have led to temporary extirpation of corals at the family level (Lovell 1989). All these factors, as well as the risk of introduction of invasive species, are potentially relevant to the sea anemone fauna of Moreton Bay.
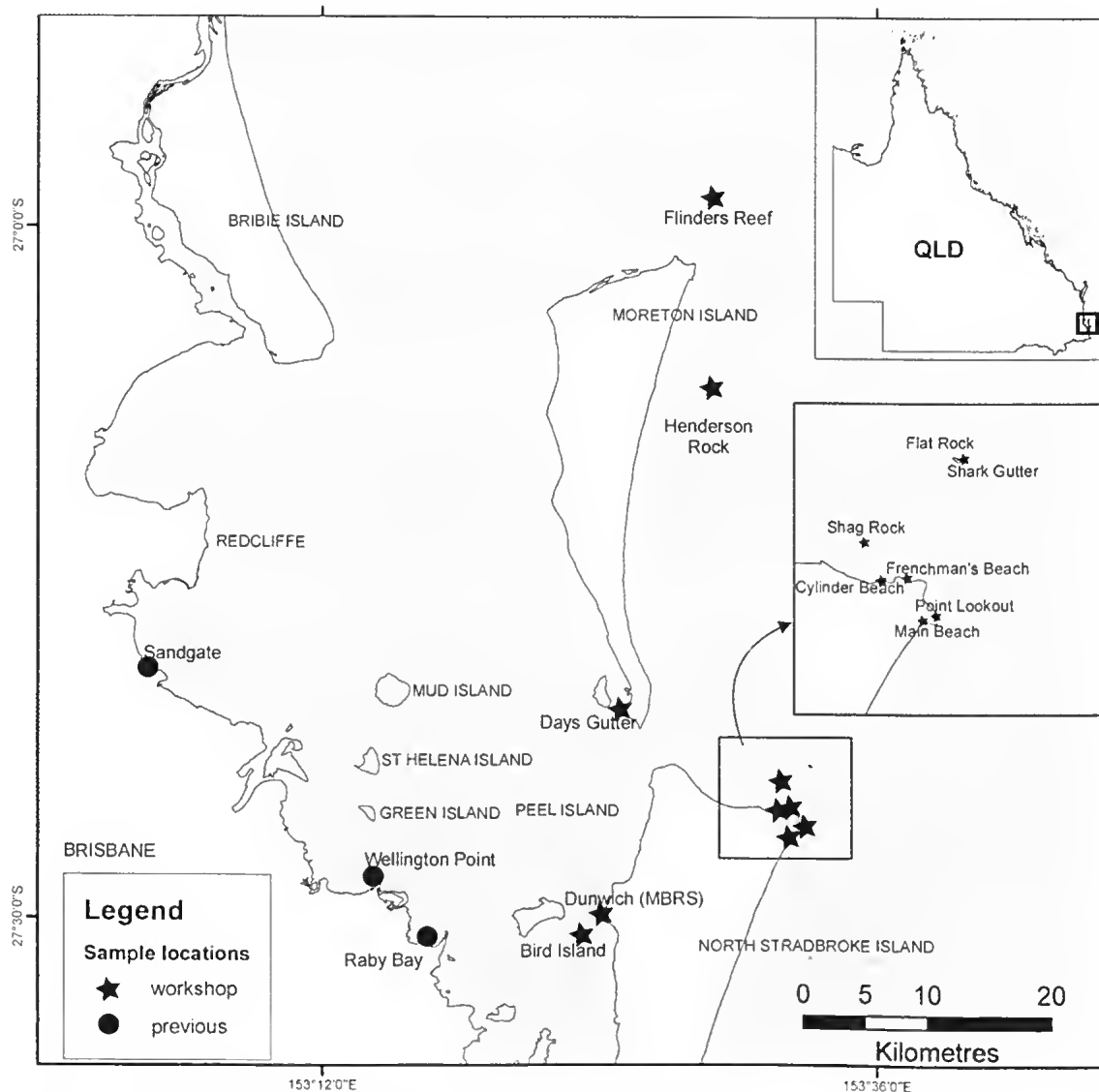
FIG. 1. Map of the Moreton Bay region, indicating locations of specimens reported in this account. MBRS = Moreton Bay Research Station of the University of Queensland, base for The Thirteenth International Marine Biological Workshop. Two locations not shown, Caloundra and Point Cartwright lie just to the north.

Australia's sea anemones have had scant attention in comparison with other members of Anthozoa (especially scleractinian corals and octocorals). The 110 species of anemones recorded from Australia, including its Antarctic waters (Fautin 2008), have been estimated to represent perhaps half of Australia's actiniarians (Wolstenholme & Wallace 2004). As is true for sea anemones in most parts of Australia, large- to medium-sized shallow-water species of Moreton Bay have been documented (e.g. Hadley 1973;

Richardson *et al.* 1997), but some smaller, cryptic, or deeper water species may have been overlooked. Eight species of Actiniaria are mentioned in a guide to the Moreton Bay biota (Davie *et al.* 1998): *Actinia tenebrosa, Oulactis muscosa,* and *Aulactinia veratra* (rocky shores), the swimming anemone *Boloceroides mcmurrichi* (coastal wetlands), and anemonefish hosts *Stichodactyla haddoni* and *Macrodactyla doreensis* (sand, mud, and seagrass), and *Entacmaea quadricolor* and *Heteractis crispa* (coral reefs).

MATERIALS AND METHODS

SITES, HABITATS, AND COLLECTING METHODS

Sites sampled during the Moreton Bay International Marine Biological Workshop were within and immediately outside Moreton Bay (approx. 26°50' to 27°50'S and 153°13' to 153°26'E) (Fig. 1). Habitats included intertidal mud and sand flats (Fig. 2A), rocky reefs, platforms, and outcrops adjacent to sandy beaches (Fig. 2B), and subtidal fringing coral reefs. Collecting was done mainly by hand, either at low tide or by SCUBA diving, although some specimens were obtained from samples taken during the dredging program of the Workshop.

TAXONOMIC INFORMATION

Appearance in life is described from specimens from Moreton Bay and surrounding waters. Terminology follows Carlgren (1949); explanations and illustrations of most terms can be found in Fautin & Mariscal (1991) and Tangney *et al.* (2007). Bibliographic and published distributional information comes from the database 'Hexacorallians of the World' (Fautin 2008). Definitions of higher taxa are taken from Carlgren (1949) or published updates, some reworded or reformatted for consistency; nomenclatural and type specimen data are from Fautin *et al.* (2007b).

MATERIAL EXAMINED

Specimens collected during the Workshop were deposited in the Museum of Tropical Queensland (MTQ), Townsville, a campus of the Queensland Museum. Additional specimens from Moreton Bay were examined in the collections of the Queensland Museum, Brisbane (QM) and the Australian Museum, Sydney (AM). Previously unpublished occurrence records from elsewhere in Australia come from specimens collected by us and others during 2005 and 2006 from Queensland, Northern Territory, and around Sydney, New South Wales, and specimens we examined in the Museum and Art Gallery of the Northern Territory, Darwin (NTM), MTQ, South Australian Museum (SAM), Queen Victoria Museum and Art Gallery, Launceston (QVM), and Western Australian Museum (WAM). Type specimens examined by Daphne G. Fautin in museums worldwide (abbreviations below) are mentioned in the text. Those who assisted in collecting the material reported here are: Robert W. Buddemeier (RWB), Andrea L. Crowther (ALC), Daphne G. Fautin (DGF), Michela Mitchell (MM), Paul R. Muir (PRM), and Carden C. Wallace (CCW).

Specimens were photographed live in the field wherever possible, and most were returned to the laboratory where they were examined alive and/or preserved for taxonomically important details. For most specimens, nematocysts from tentacles, actinopharynx, mesenterial filaments, column, and, if present, acrorhagi and acontia were measured. Specimens to be deposited in museums were relaxed in isotonic magnesium chloride/sea water solution, and fixed in 10% formalin. Histological sections were cut from some specimens, and stained with Mallory Heidenhain Trichrome.

Our report does not include members of the family Edwardsiidae — worm-like, burrowing anemones. Specimens of this family were sent to Marymegan Daly, who is revising the family and will include the Moreton Bay material in her study.

MUSEUMS

Museums from which type material was examined by DGF, in addition to those listed above, are: American Museum of Natural History, New York, New York, USA (AMNH); Bernice P. Bishop Museum, Honolulu, Hawai'i, USA (BPBM); Natural History Museum, London, UK (BMNH); California Academy of Sciences, San Francisco, California, USA (CAS); Canterbury Museum, Christchurch, New Zealand (CM); Museum für Naturkunde der Humboldt Universität, Berlin, Germany (MNB); Museum of Zoology, Lund University, Sweden (LO); Natural History Museum, Göteborg, Sweden (NHMG); Phyletisches Museum, Jena, Germany (PMJ); Senckenberg Museum, Frankfurt am Main, Germany (SMF); Swedish Museum of Natural History, Stockholm, Sweden (SMNH); University of Kansas Natural History Museum, Lawrence, Kansas, USA (KUNHM); University Museum of Zoology, Cambridge, UK (UMZ); Yale Peabody Museum, New Haven, Connecticut, USA (YPM); and Zoologisches Museum, Hamburg, Germany (ZMH).

RESULTS AND DISCUSSION

Eighteen species of Actiniaria were recorded in and around Moreton Bay (Table 1), and an additional species identified only to the genus

Diadumene. This is not a complete inventory of Moreton Bay sea anemones. Aside from the edwardsiids, the identity of some species has not been resolved, including one that was photographed in the field but not collected, and one that is taxonomically problematic and will be the subject of a separate publication. New records for Australia are *Anthopleura handi* and *A. buddemeieri*; *A. handi* is common in the rocky intertidal zone on protected sites inside Moreton Bay, and *A. buddemeieri* occurs on exposed beach sites outside the Bay. We include other new Australian records of these species from the Northern Territory and the Sydney region of New South Wales. *Verrillactis paguri* is also newly recorded from Australia. *Actinia australiensis*, previously known only from New South Wales, is newly recorded from Moreton Bay. The unidentified species of *Diadumene* is possibly new to science; anemones of this genus, which is a well-known invasive (e.g. Zabin *et al.* 2004), have not previously been recorded from Australia to our knowledge.

The record of sea anemones new for Moreton Bay and, in some cases, for Australia, is an important step in the documentation of Australia's anemone fauna, and the role of these animals in coastal ecosystems.

Actiniarians from the Moreton Bay region include 14 predominantly tropical species and four pre-dominantly temperate species (Table 1). The presence of these two faunal types is a characteristic of the region's biota (Davie & Hooper 1998; Tibbetts *et al.* 1998; Dennison & Abal 1999). This finding was also true of other taxa studied by participants in the Moreton Bay Workshop.

The Workshop inventory of marine organisms forms an important baseline. Moreton Bay, at the interface of tropical and temperate faunas of eastern Australia, represents a vital part of the eastern Australian coastal zone, which must be continuously monitored for changes in species diversity, altered competition for habitat and resources, and species extinctions and arrivals associated with global climate change. It is possible that tropical sea anemones not currently present in the region might expand southwards in response to elevated sea surface temperatures associated with climate change. This may introduce competition for resources and thus have an impact on species currently present in the Bay. Warmer conditions may also affect distribution of temperate species, most of which (from records so far) are concentrated in shallow water. Pressure on the Bay due to the demands of a rapidly growing human population will increase alongside the ameliorating effects of changes such as improvements in habitat conditions and/or water quality due to marine protected areas, cessation of coral mining, and other

A

B
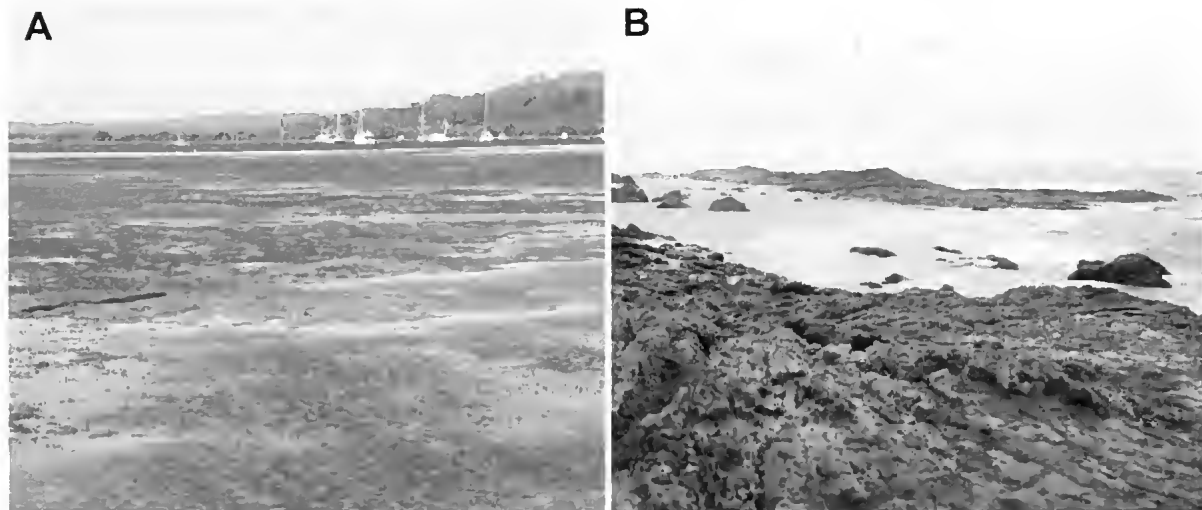
FIG. 2. Examples of intertidal sampling sites at Moreton Bay, photographed at low tide. **A**, mud-sand flat, Dunwich, North Stradbroke Island, showing eelgrass (*Zostera capricorni*). **B**, wave-exposed rocky outcrops on sandy beach, Frenchman's Beach, North Stradbroke Island.

Table 1. Distribution in the Moreton Bay region of the 18 species of actiniarians identified to species.

Species	Soft substratum; intertidal, shallow subtidal	Rocky inter-tidal	Reefal	Hermit crab associates
Tropical to subtropical				
Anthopleura buddemeieri Fautin, 2005		x		
Anthopleura handi Dunn, 1978		x		
Boloceroides mcmurrichi (Kwietniewski, 1898)	x		x	
Calliactis polypus (Forsskål, 1775)				x
Entacmaea quadricolor (Leuckart in Rüppell & Leuckart, 1828)			x	
Gyractis sesere (Haddon & Shackleton, 1893)		x		
Heteractis crispa (Hemprich & Ehrenberg in Ehrenberg, 1834)	x		x	
Heteractis malu (Haddon & Shackleton, 1893)	x		x	
Heteranthus verruculatus Klunzinger, 1877		x	x	
Macrodactyla doreensis (Quoy & Gaimard, 1833)	x		x	
Stichodactyla haddoni (Saville-Kent, 1893)	x			
Stichodactyla tapetum (Hemprich & Ehrenberg in Ehrenberg, 1834)	x			
Triactis producta Klunzinger, 1877			x	
Verrillactis paguri (Verrill, 1869)				x
Temperate to subtropical				
Actinia australiensis Carlgren, 1950		x		
Actinia tenebrosa Farquhar, 1898		x		
Aulactinia veratra (Drayton in Dana, 1846)		x		
Oulactis muscosa (Drayton in Dana, 1846)		x		

environmental initiatives associated with the Moreton Bay Marine Park (Harrison *et al.* 1998). Success in managing the marine park and enhancement of water quality and other factors will be critical to ensuring that these changes take place against a background of maximal environmental quality.

Species recorded only on the ocean side of North Stradbroke Island, particularly subtidal species associated with coral reefs (*Entacmaea quadricolor, Heteractis* spp., see Table 1), might be expected to establish themselves inside the Bay in response to improved conditions. In the case of corals, entry or re-entry of species is already occurring (C. Wallace, I. Fellegara & P. Harrison pers. comm.), possibly enhanced by the absence of spikes in freshwater input into the Bay due to several recent seasons of low rainfall in the catchment regions.

Key to Living Sea Anemones of Moreton Bay

This key uses characters such as behaviour, posture, stickiness, and colour that disappear in preservation. But beware that tentacle form (length, existence of bulbs) may change while the animal is alive. There may be 2, 3, or 5 choices at each junction point.

1. Tentacles not deciduous. 2
— Tentacles deciduous, can move in coordinated rowing motion to effect swimming; so

numerous they hide oral disc and may hide entire animal; each tentacle pointed. Column typically less than 10 mm long. . . . .
. . . . *Boloceroides mcmurrichi*

2. Tentacles all alike. 3
— Tentacles of two distinct types. Discal tentacles sparse, papillose; marginal ones longer, slender. . . *Heteranthus verruculatus*

3. No acontia. 4
— Pink or salmon acontia can be emitted through cinclides located proximally; pedal disc attached to gastropod shell; column length and base diameter similar. . . . . .
. . . . *Calliactis polypus*
— White acontia not readily emitted. Attached at columella or aperture of gastropod shell; pedal disc very broad relative to column; tentacles short, stubby, white; column white.
. . . . *Verrillactis paguri*

4. Each tentacle lacking a bulb although its end may be blunt or swollen. 5
— Tentacles brown, cylindrical; some or all may have terminal or subterminal bulb tipped with red. Column typically brown. Animals may be clonal. Expanded oral disc broader than pedal disc; expanded diameter typically greater than 80 mm. . . . .
. . . . *Eutacmaea quadricolor*

5. Column smooth. 6
— Column with verrucae, to which debris may adhere. 7
— Column with branched outgrowths that bear stalked spheres. . . . . . . *Triactis producta*

6. Column, oral disc, tentacles dull red; each tentacle with blue-grey tip, oral disc flecked with white. . . . . . . *Actinia australiensis*
— Column and oral disc typically brown to maroon; tentacles bright solid red. . . . . .
. . . . *Actinia tenebrosa*

7. Expanded oral disc much broader than pedal disc. 8
— Expanded oral disc not much broader than pedal disc. 11

8. Tentacles short, cover most of oral disc. . 9
— Tentacles long, tentacles sparse on central oral disc, most at margin. 10

9. Oral disc flat, usually less than 100 mm diameter, tentacles arranged in distinct fields, may be so crowded that each resembles a kernel of maize. . . . *Stichodactyla tapetum*

— Flat to wavy oral disc usually greater than 100 mm diameter, densely covered with sticky tentacles, each pointed or with blunt to mildly swollen end; exocoelic tentacles maybe more robust than endocoelic ones. .
. . . . *Stichodactyla haddoni*

10. Column thin with eye-shaped verrucae; long tentacles sparse, may assume cork screw form, each inner one brown, may have light longitudinal stripe; oral disc may be brown with radial light stripes. . . . . .
. . . . *Macrodactyla doreensis*
— Column thin, flared, with few verrucae per row; tentacles short, sparse; distal column violet-brown, lower column may be solid or splotched with yellow, orange or red. . .
. . . . *Heteractis malu*
— Column thick, leathery, flared, with many verrucae per row; distal column grey-white. Tentacles abundant, normally long. . . . .
. . . . *Heteractis crispa*

11. Column grey with attached shell grit; acrorhagi marginal, large, white, feathery.
. . . . *Oulactis muscosa*
— Column grey with red punctations, the proximal ones simply pigment spots; to 25 mm in length and pedal disc diameter.. . . . . . .
. . . . *Anthopleura buddemeieri*
— Column beige, 15–30 mm in diameter; oral disc grey; tentacles to 30 mm long, with light bars across them. . . *Anthopleura handi*
— Column green or brown, 50–60 mm in diameter; tentacles to 40 mm long, rusty red or green or light brown. . *Aulactinia veratra*
— Column grey, oral disc greenish; tentacles without bars, more than 100 in number. . .
. . . . *Gyractis sesere*

SYSTEMATIC TREATMENT

BOLOCEROIDIDAE

Boloceroides Carlgren, 1899

Definition. Pedal disc present but lacking basilar muscles; column smooth, lacking outgrowths; no marginal sphincter muscle; no distinct siphonoglyphs. Inner tentacles much longer than marginal ones; tentacles non-retractile; each with basal sphincter muscle that allows tentacle to be cast off. Longitudinal muscles of tentacles and column, and radial muscles of oral disc ectodermal; mesenterial retractor muscles weak. Six
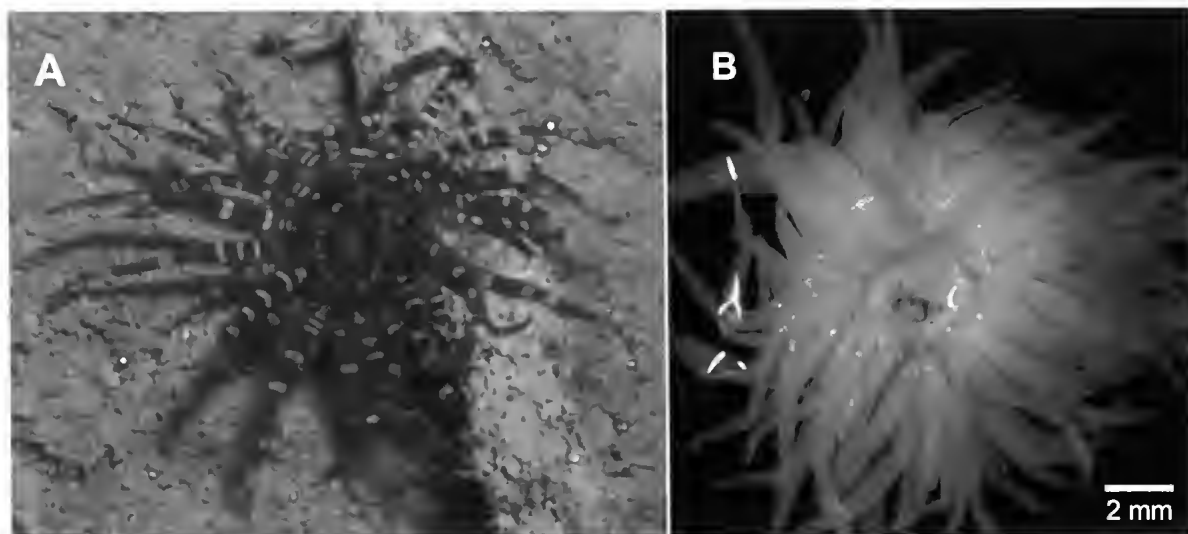
FIG. 3. *Boloceroides mcmurrichi*. **A**, live animal from Boggy Ck, Myrtletown, mouth of the Brisbane River (Photo QM). **B**, preserved specimen, MTQ-G59757, from Magnetic I., north Queensland, showing many tentacles.

pairs of mesenteries commonly complete, but more may be present in asexually-produced individuals; more mesenteries distally than proximally. All mesenteries except directives may be fertile. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic amastigophores. Spirocysts occur in the column. Capable of swimming by rowing movements of tentacles.

Type species: *Bolocera mcmurrichi* Kwietniewski, 1898.

Boloceroides mcmurrichi (Kwietniewski, 1898)
(Fig. 3)

Bolocera mc murrichi Kwietniewski, 1898: 387, 389, 394–395, pl. 25, figs 10–11.
Boloceroides hermaphroditica Carlgren, 1900: 18–19.
Nectothela lilae Verrill, 1928: 14, fig. 2d–f.

Material Examined. HOLOTYPE: *Nectothela lilae*, AMNH-1476, Malaekahana, Oahu, Hawai'ian Islands. OTHER MATERIAL: *Moreton Bay*. Flat Rock, North Stradbroke I., M. Preker, 17.02.2005 (disintegrated). *Australia Elsewhere*. MTQ-G55344, Pallarenda, NE Qld; MTQ-G59757, 5 spec., Cockle Bay, Magnetic I., NE Qld; NTM-C5550–51, South Shell I., Darwin, NT, 1988; NTM-C10072, East Point Sponge Gardens, Darwin, NT, 1990; NTM-C11907, Nhulunbuy (Gove), NT, 1971; NTM-C12767, Darwin Harbour, NT, 1999; NTM-C14766, Bathurst I., NT, 2003; NTM-C13653, Darwin, NT.

Appearance. Pedal disc weakly adherent. Column thin-walled, translucent, to 10 mm long. Tentacles pointed, not all same size; transparent with or without white or cream transverse stripes; number variable, usually around 200 (Fig. 3), but as few as 12 in the Moreton Bay specimen examined from North Stradbroke Island.

Habitat. Lower intertidal and shallow subtidal of muddy or sandy areas; attaches to surfaces including mangroves and seagrasses. Observed attached to seagrass blades in seagrass meadows at Dunwich near the Moreton Bay Marine Station in 2001, by I. Lawn, M. Preker & ALC.

Distribution. Red Sea; Eastern Africa; Singapore; Western Australia; Northern Territory; eastern Australia; Indonesia; Papua New Guinea; French Polynesia; Hawai'i. Type locality: Ambon, Indonesia.

Comments. Because of its fragility, and perhaps seasonality of occurrence, this species is poorly represented in museum collections and seldom recorded in surveys. However, anecdotal evidence suggests it is not uncommon in Moreton Bay, and the specimen photographed by Davie (1998: 36) (Fig. 3A) was collected from a small muddy mangrove creek at the mouth of the Brisbane River (P. Davie, pers. comm.). It can cast off its tentacles, which regrow, accounting for the variability in number and size. DGF observed this species attached to the coral *Acropora* in Madang Lagoon, Papua New Guinea, in the late 1980s.

Further literature. TAXONOMY & DISTRIBUTION: Carlgren (1924a); Fishelson (1970); Doumenc (1973);

FIG. 4. *Actinia australiensis* from Frenchman's Beach, North Stradbroke Island. **A**, several individuals on under-surface of rock: note white flecks at base of tentacles. **B**, individual on dead oyster shell: two bright red siphonoglyphs (si) are visible.

Cutress (1977); Dunn (1982); Fautin (1988); Davie *et al.* (1998); Paulay *et al.* (2003). ECOLOGY & BEHAVIOUR: Lawn & Ross (1982); den Hartog (1997a); Erhardt & Knop (2005).

ACTINIIDAE

Actinia Linnaeus, 1767

Definition. Pedal disc wide. Column low, smooth; fosse deep, containing simple or slightly compound marginal spherules. Endodermal marginal sphincter muscle weak or strong, diffuse, rarely with slight tendency to be meso-endodermal. Tentacles retractile; longitudinal muscles ectodermal. Mesenteries more numerous basally than marginally; all stronger ones except directives fertile; mesenterial retractor muscles diffuse. Cnidom: spirocysts, holotrichs, basitrichs, microbasic *p*-mastigophores.

Type species: *Priapus equinus* Linnaeus, 1758.

Actinia australiensis Carlgren, 1950

(Fig. 4)

Actinia australiensis Carlgren, 1950a: 132–133, fig. 1.

Material Examined. SYNTYPES: LO-324-Kat 1, 11 spec., Sydney district, NSW, Australia; LO-324-Kat 2, 2 spec., along NSW coast, Australia. OTHER MATERIAL: *Moreton Bay*. MTQ-G55345, Frenchman's Beach, North Stradbroke I., J. Phillips, 2005; MTQ-G55347, Frenchman's Beach, North Stradbroke I., DGF, PRM, ALC, 2005; MTQ-G59390, Frenchman's Beach, North Stradbroke I., DGF, 2005; MTQ-G55346, Cylinder Beach, North Stradbroke I., DGF *et al.*, 2005; MTQ-G55348, Main Beach, North Stradbroke I., MM *et al.*, 2005. *Australia Elsewhere*. AM-G16963, Newport rock platform, NSW, K. Attwood & CCW, 2005.

Appearance. Pedal disc at least as broad as oral disc. Column red, to 30 mm long; may be slightly corrugated longitudinally. Oral disc flat, about half as broad as extended column length; red with white flecks near base of tentacles (Fig. 4A). Approximately 96 pointed tentacles, red with bluish-purple tips, hexamerously arranged; inner held upward, about half as long as oral disc diameter; outer shorter, extended horizontally. Fosse deep in life, may appear shallow in preserved specimens; to 48 whitish marginal spherules. Actinopharynx usually with two siphonoglyphs (Fig. 4B), in some specimens only one.

Habitat. Intertidal on rocks in surf zone, especially on underside of rocks and in crevices around low water mark.

Distribution. New South Wales; southeast Queensland. Type locality: Sydney, NSW, Australia.

Comments. Carlgren (1950a) described two colour variants, one as above. The other, having a light olive-green or light brown column with white streaks, and reddish brown tentacles, was not seen in Moreton Bay. Although this species occurs along the entire New South Wales coast, this appears to be the first record of it in Queensland.

Actinia tenebrosa Farquhar, 1898

(Fig. 5)

Actinia tenebrosa Farquhar, 1898: 527, 535–536.
Actinia c.f. *equina* — Blackburn, 1937: 369.

Material Examined. HOLOTYPE: CM-AQ3271, near Wellington, New Zealand. OTHER MATERIAL: *Moreton*
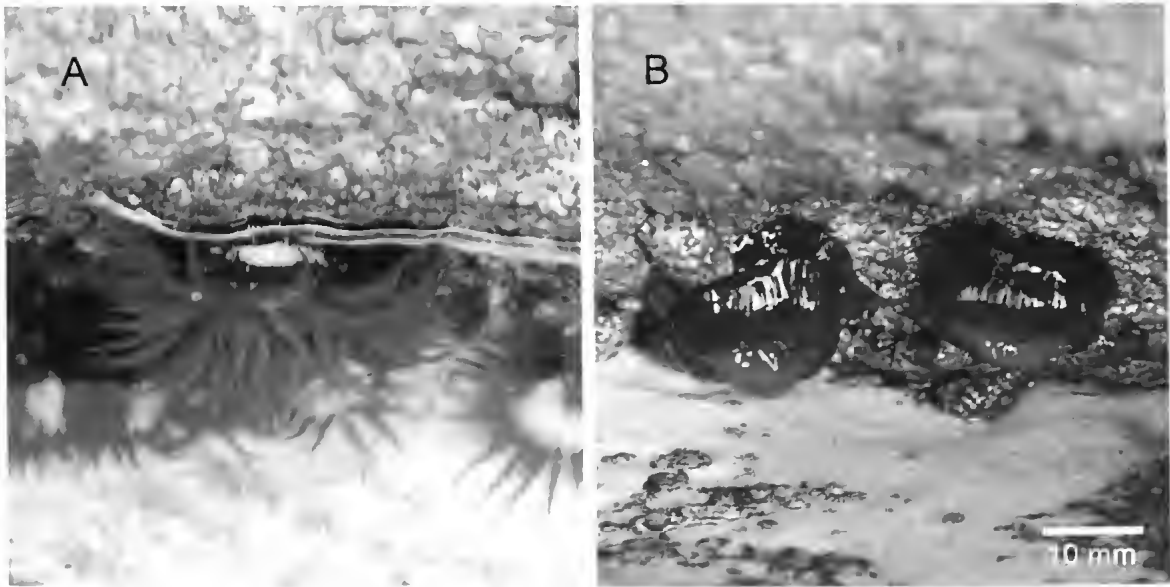
FIG. 5. *Actinia tenebrosa* from rock crevice at Frenchman's Beach, North Stradbroke Island. **A,** individual with tentacles expanded (anemones in background are *Aulactinia veratra*). **B,** two individuals with tentacles contracted at low tide. (photographs: P. Davie)

Bay. MTQ-G58751, Frenchman's Beach, North Stradbroke I., ALC & DGF, 2005; QM-G10529, Caloundra, 1951; QM-G304910, Point Cartwright, Mooloolaba; QM-G317223, Point Lookout, North Stradbroke I., J.N.A. Hooper *et al.*, 2000. *Australia Elsewhere*. AM-G15825, Long Reef, Colloroy, NSW, 1962; AM-G16869, Second Head, Forster, NSW, 2003; AM-G16966, Newport, NSW, M. Capa, 2005; QVM-20:580, Falmouth, Tasmania, 1993; QVM-29:1784, Beechport, Tasmania, 1993; QVM-20:1785, Sandy Point, Tasmania, Bridgeport, 1993. SAM-K3638, 3 spec., Kingston, South Australia, 1941.

Appearance. Pedal disc to approx. 40 mm diameter. Column dark maroon, to 30 mm long. Tentacles to 144, bright red, tapered to a point. Marginal spherules 24, bright blue, usually deep within the fosse. Actinopharynx with two siphonoglyphs. Sphincter muscle diffuse. Longitudinal muscles weak. See Carlgren (1924b) for anatomical details.

Habitat. Intertidal on rocks in surf zone, especially on underside of rocks and in crevices around low water mark.

Distribution. Western, southern, and eastern Australia from Shark Bay, Western Australia to Heron Island, central Queensland; New Zealand. Type locality: near Wellington, New Zealand.

Comments. One of the commonest and most easily identified Australian coastal species,

Actinia tenebrosa is not well represented in museum collections. It can be distinguished in life by its patternless smooth maroon column, red tentacles and oral disc, and blue marginal spherules. It is often referred to as the Waratah Anemone due to the striking red colour of the tentacles. The young are brooded internally until they attain a considerable size. Some of the references below contain detailed anatomical descriptions. In referring to this species as *A. equina*, Blackburn (1937: 369) remarked, 'there seems, however, no more justification for separating [*A. tenebrosa*] than for many other colour varieties of *A. equina*.'

Further literature. TAXONOMY & DISTRIBUTION: Stuckey (1909); Stuckey & Walton (1910); Carlgren (1924b, 1950a, b, 1954); Blackburn (1937); Parry (1951); Cutress (1971); Ottaway (1975); Dunn (1982); Dawson (1992). BIOLOGY & ECOLOGY: Ottaway (1973, 1979a, b); Black & Johnson (1979); Ayre (1983, 1984a, b, 1995); Bennett (1987); Ayre *et al.* (1991); Edgar (1997); Sherman & Ayre (2008).

Anthopleura Duchassaing & Michelotti, 1860

Definition. Pedal disc well developed. Column with adhesive verrucae arranged in more or less distinct longitudinal rows, especially in its upper part. Marginal spherules present. Endodermal marginal sphincter muscle weak or
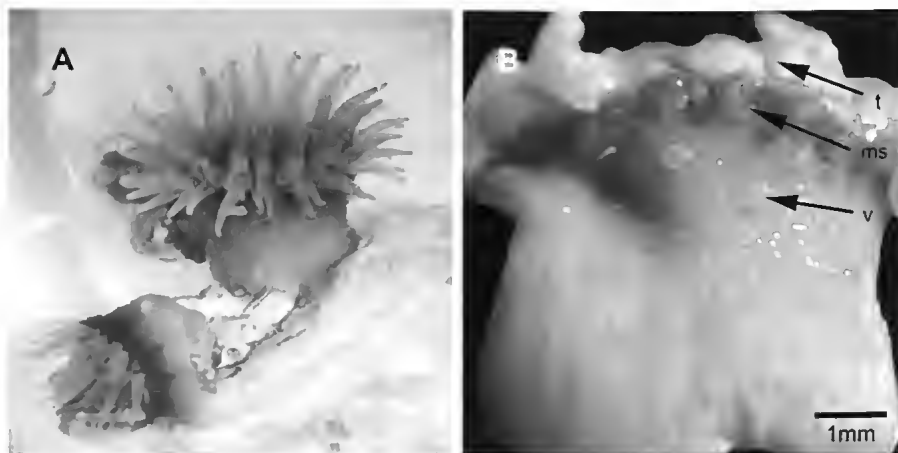
FIG. 6. *Anthopleura buddemeieri* from Main Beach, North Stradbroke I. **A,** two individuals on rock in laboratory (photograph: I. Lawn). **B,** preserved specimen, MTQ-G58753, showing column with arrows indicating adhesive verruca (v), marginal spherule (ms), and tentacle (t).

strong, restricted to circumscribed. Tentacles simple, hexamerously or irregularly arranged, their longitudinal muscles ectodermal or meso-ectodermal. Numerous complete mesenteries, all the stronger ones fertile; mesenteries grow from base; retractor muscles of the stronger mesenteries diffuse, sometimes restricted. Cnidom: spirocysts, holotrichs, basitrichs, microbasic *p*-mastigophores.

Type species: *Anthopleura krebsi* Duchassaing & Michelotti, 1860.

Anthopleura buddemeieri Fautin, 2005
(Fig. 6)

Anthopleura buddemeieri Fautin, 2005: 379–389, figs 1–5.

Material Examined. HOLOTYPE: KUNHM-001992, Wongat I., Madang Lagoon, Madang, Papua New Guinea. PARATYPES: As listed in Fautin (2005, 2008). OTHER MATERIAL: *Moreton Bay*. MTQ-G55349, Frenchman's Beach, North Stradbroke I., J. Phillips, 2005; MTQ-G55350, Cylinder Beach, North Stradbroke I., DGF *et al.*, 2005; MTQ-G58753, Main Beach, North Stradbroke I., MM *et al.*, 2005. *Australia Elsewhere*. AM-G16965, Newport Beach, NSW, M. Capa, 2005.

Appearance. Pedal disc approx. same diameter as column. Column 9–12 mm long, 7–8 mm greatest diameter; grey (darker distally), with red verrucae distally, red punctations proximally. Fosse deep. Oral disc with central mouth raised on cone, two siphonoglyphs. Pale yellow-brown tentacles approx. 50, in 2–3 cycles, slender,

tapering to blunt point, all approx. 5 mm long, 1 mm wide. Oral stomata large, marginal stomata small or absent.

Habitat. Attached to rock walls and platforms in high-energy surf areas. One specimen was attached to the red alga *Pterocladiella capitacea* growing on rocks.

Distribution. Fiji; Papua New Guinea; eastern Australia (Moreton Bay and Sydney region); Singapore. Type locality: Wongat Island, Madang Lagoon, Madang, Papua New Guinea.

Comments. These are the first records of this species from Australia.

Further literature. TAXONOMY & DISTRIBUTION: Fautin (2005).

Anthopleura handi Dunn, 1978
(Fig. 7)

Anthopleura handi Dunn, 1978: 54–63, figs 1–8.

Material Examined. HOLOTYPE: CAS-15674, Jeram Beach, Strait of Malacca, Selangor, Peninsular Malaysia. PARATYPES: all from type locality; BPBM-D5t5; BPBM-D516; BPBM-D517, 3 specs; CAS-15675; CAS-15676; CAS-15677; USNM-56557; USNM-56558. OTHER MATERIAL: *Moreton Bay*. MTQ-G58747, 2 spec., Dunwich, DGF & ALC, 2005; MTQ-G58759, 5 spec., Moreton Bay, 2005. *Australia Elsewhere*. NTM-C3584, Ludmilla Creek, Darwin, NT, 1982; NTM-C2263, no data; NTM-C2920, Creek 'H', East Arm, Ludmilla Creek, Darwin, NT, 1984.

Appearance. Column of specimens examined 14 mm long, 9 mm wide; grey with lighter verrucae

FIG. 7. *Anthopleura handi* from Dunwich, North Stradbroke Island. **A,** oral disc of living animal *in situ*, showing long, narrow tentacles with white blotches. **B,** side view of living animal *in situ*, showing broad pedal disc (pd) and sand grains adhering to verrucae (v). **C,** Preserved specimen, MTQ-G58747, showing verruca (v).

arrayed longitudinally; acrorhagus at distal end of each column of verrucae. Oral disc with slit-like mouth. Grey tentacles approx. 60; length to 30 mm, diameter approx. 2 mm at base; inner with white flecks and cross-bars (Fig. 7A). Fosse deep. Actinopharynx usually with two siphono-glyphs. Broods young internally.

Habitat. Attached to rock or oyster shells on intertidal mud flats, including the high intertidal regions, where the anemones occur around the base of rocks.

Distribution. Malaysia; Singapore; Philippines; northern and eastern Australia. Type locality: Jeram Beach, Strait of Malacca, Selangor, Peninsular Malaysia.

Comments. These are the first records of *A. handi* from Australia.

Further literature. TAXONOMY & DISTRIBUTION: England (1987); Fautin (1988). BIOLOGY & ECOL OGY: Dunn (1982).

Aulactinia Verrill, 1864

Definition. Pedal disc well developed, capable of distension. Column elongated, moderately contractile; upper part covered with prominent verrucae in longitudinal rows, the uppermost one in each row situated just below the tentacles, larger than the others, and lobed; foreign material often attached to verrucae. Tentacles numerous, simple, short. Marginal pseudo-spherules may be present. Mesenteries well developed, much narrower near the base, thickened above with strong longitudinal muscles. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Aulactinia capitata* Agassiz in Verrill, 1864.

Aulactinia veratra (Drayton in Dana, 1846)
(Fig. 8)

Actinia veratra Drayton in Dana, 1846: 129–130.
Cribrina verruculata Lager, 1911: 233–234.

Material Examined. SYNTYPE: *Cribrina verruculata*, MNB-5450, east coast of Rottnest I., WA. OTHER MATERIAL: *Moreton Bay.* MTQ-G58752, Frenchman's Beach, North Stradbroke I., DGF & ALC, 2005; MTQ-G58755, Cylinder Beach, North Stradbroke I., DGF *et al.*, 2005; QM-G304911, Point Cartwright, Mooloolaba; MTQ-G60025, Point Arkright, Coolum, 2007. *Australia Elsewhere.* AM-G16870, Second Head, Forster, NSW, 2003; AM-G17453, 5 spec., Tasmania, 1958; AM-G16960, 4 spec., Newport, NSW, 2005.

Appearance. Expanded pedal disc diameter to 45 mm. Column to 60 mm expanded length, dark green to deep brown. Flat oral disc same colour as column, to 40 mm diameter. Tentacles tapered, brown, brownish red, or brownish green, hexamerously arranged; inner 20 mm long, outer to 30 mm long, may coil at ends.

Habitat. Intertidal rocks in surf zone, especially on underside and in crevices around low water mark.

Distribution. Southern Australia from Perth, Western Australia. to southeast Queensland. Type locality: Wollongong, NSW, Australia.

Comments. Retracted specimens of this species may appear black.

Further literature. TAXONOMY & DISTRIBUTION: Carlgren (1950a, b, 1954); Ottaway (1975); Edmands & Fautin (1991); Dawson (1992).
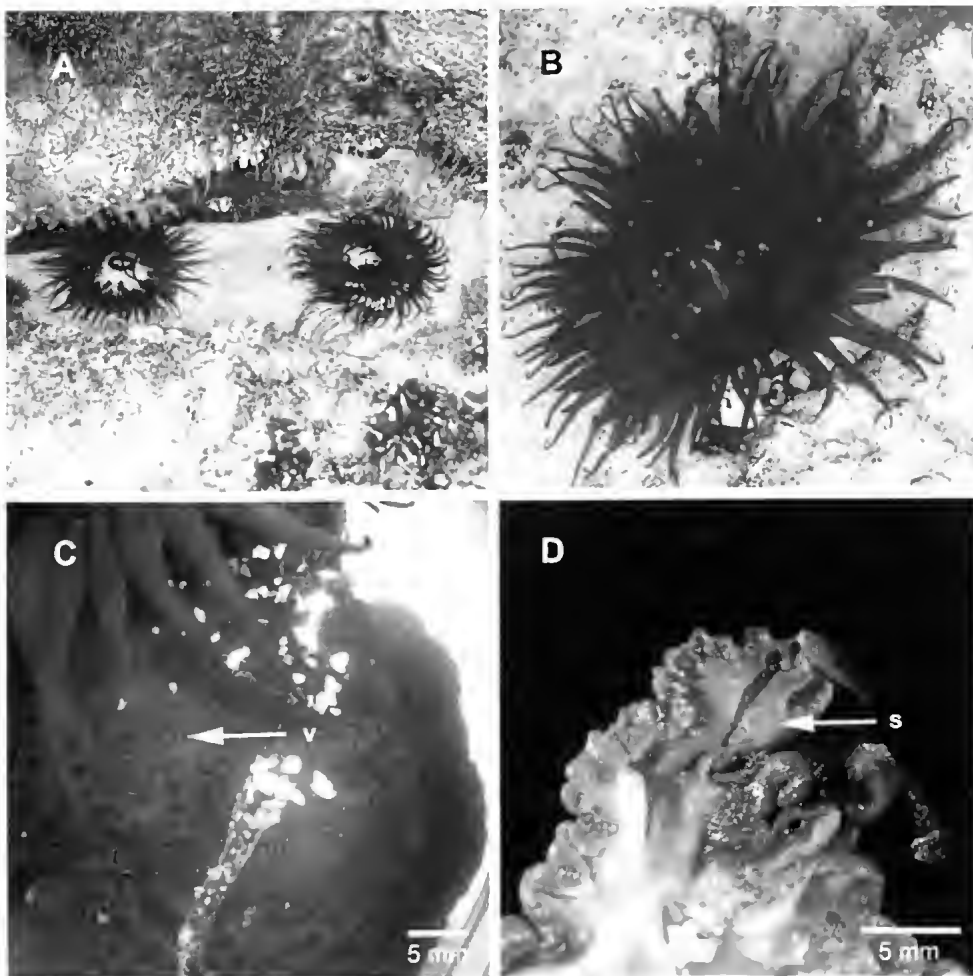
FIG. 8. *Aulactinia veratra* from Frenchman's Beach, North Stradbroke I. **A**, specimens in rock crevice. **B**, oral disc of living animal; note numerous long tentacles, the marginal ones held outward, and the inner ones held perpendicular to oral disc. **C**, living animal in laboratory, specimen showing column with verrucae (v) (photograph: I. Lawn); **D**, preserved specimen, MTQ-G58752, dissected to show circumscribed endodermal marginal sphincter muscle(s).

Entacmaea Ehrenberg, 1834

Definition. Pedal disc well developed. Column smooth; margin distinct, lacking spherules or pseudospherules; fosse generally deep. Endodermal marginal sphincter muscle diffuse, sometimes weak, in rare cases some lamellae invade mesogloea. Inner tentacles longer than outer; longitudinal muscles ectodermal, circular muscles endodermal. Number of siphonoglyphs variable. Mesenteries numerous, many complete, all stronger ones including directives fertile; mesenteries added at margin; a pair of directives usually connected to each siphonoglyph; retractor muscles diffuse, often band-like. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Actinia quadricolor* Leuckart in Rüppell & Leuckart, 1828.

Entacmaea quadricolor (Leuckart in Rüppell & Leuckart, 1828)
(Fig. 9)

Actinia quadricolor Leuckart in Rüppell & Leuckart, 1828: 4–5, fig. 3.
Actinia vas Quoy & Gaimard, 1833: 147–148, pl. 12, fig. 6.

Actinia erythrosoma Hemprich & Ehrenberg in Ehrenberg, 1834: 257.

Actinia adhaerens Hemprich & Ehrenberg in Ehrenberg, 1834: 258–259.

Actinia helianthus Hemprich & Ehrenberg in Ehrenberg, 1834: 259.

Actinia ehrenbergii Brandt, 1835: 11.

Crambactis arabica Haeckel, 1876: 4, fig. 2.

Condylactis Gelam Haddon & Shackleton, 1893: 123–124.

Condylactis Ramsayi Haddon & Shackleton, 1893: 124.

Anemonia Kwoiam Haddon & Shackleton, 1893: 125–126.

Gyrostoma Hertwigi Kwietniewski, 1897: 30–34.

Gyrostoma Stuhlmanni Carlgren, 1900: 39–40, pl. 1, fig. 16.

Gyrostoma Haddoni Lager, 1911: 229–230, fig. 10.

Gyrostoma sulcatum Lager, 1911: 230–232, figs 11, 12.

Antheopsis Carlgreni Lager, 1911: 243–244, fig. 19.

Material Examined. HOLOTYPE: *Actinia quadricolor*: SMF-34, near Suez, the Red Sea, Egypt. SYNTYPES: *Anemonia kwoiam*: UMZ-Co182, Torres Strait. *Condylactis ramsayi*: UMZ-Co183, 3 spec., Torres Strait. *Gyrostoma hertwigii*: PMJ-Coel 66, 2 spec., SMNH-57, 3 pieces, Thursday I. *Gyrostoma sulcatum*: WAM-Z887, SMNH-4876, ZMH-5334, ZMH-5336, MNB-5443, MNB-5444, 2 spec., Shark Bay, WA. OTHER MATERIAL: *Moreton Bay*. MTQ: no collection but specimens photographed February 2005 (see Fig. 9). *Australia Elsewhere*. AM-G15572, Bumbra Reserve, Norfolk I., 1980; AM-G16069, 2 spec., Rundle I., Qld, 1974; AM-G16908, Northwest I., Capricorn Group, Great Barrier Reef, Qld, 1931; AM-G16975, 3 spec., Ned's Beach, Lord Howe I., 1964; NTM-C3267, C3275, Coral Bay, Port Essington, NT, 1981; NTM-C5449, Coral Bay, Port Essington, NT, 1986; NTM-C5549, South Shell I., Darwin Harbour, Darwin, NT, 1988; NTM-C11912, C11914, Shore Reef, Nightcliff, Darwin, NT, 1975; BMNH-1054.6.28.30, 3 spec., Great Barrier Reef. PMJ-Coel66, 2 spec., Thursday I., Torres Strait, Qld; SMNH-667A, 2 spec., Shark Bay, WA; WAM-29-76, 5 spec., Abrolhos, WA; WAM-33-76, 3 spec., Abrolhos, WA.

Appearance. Pedal disc well developed, usually narrower than oral disc. Column to 500 mm long, oral disc to 400 mm diameter, at least twice as broad as pedal disc. Flared column typically rich brown but may be greenish or reddish; in some specimens paler near base. Deep fosse. Flat brown, greenish, or pink oral disc may have radial white stripes around mouth; most tentacles near margin. Tentacles cylindrical, hardly tapered; inner 2–3 times as long as marginal; typically brown with greenish cast and pink or purple tip; bulb at or just below tip may have a white equator or be flecked with white.

Habitat. Reef environments; base may be attached in hole or crevice so only tentacles are visible.

Distribution. Red Sea; eastern Africa; Indian Ocean; Melanesia; Micronesia; Japan; across northern Australia from Perth, WA to northern NSW. Type locality: Near Suez, Red Sea, Egypt.
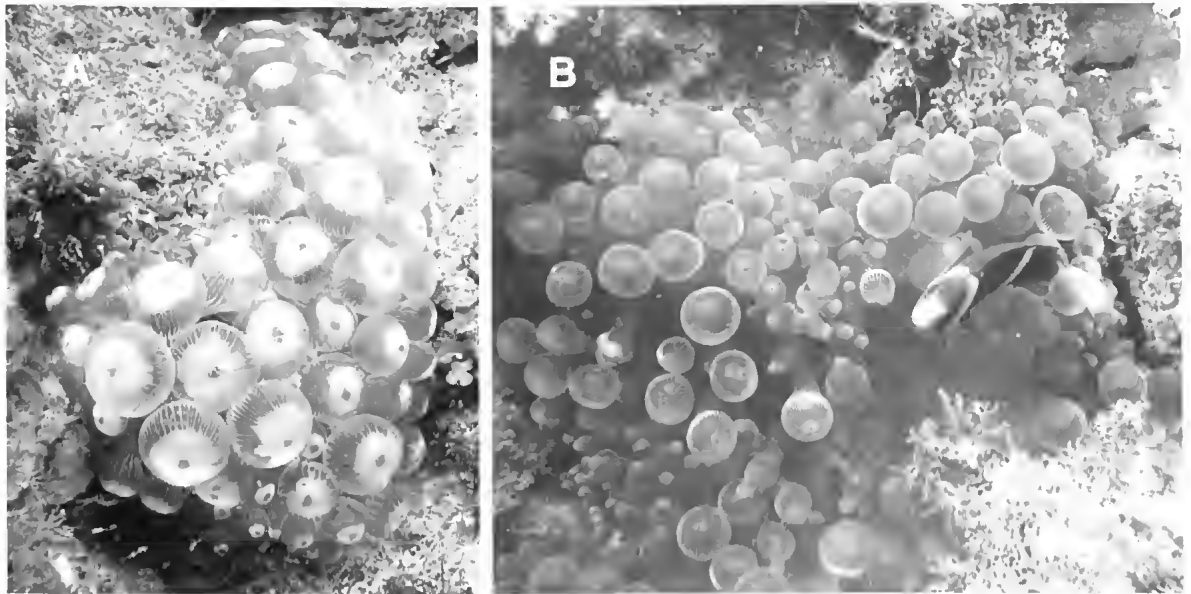
FIG. 9. *Entacmaea quadricolor* at Flat Rock, North Stradbroke I. **A**, individual with expanded tentacle tips. **B**, individual with tentacles in a range of expansion states; fish is *Amphiprion akindynos* (photographs: J. Hsieu).
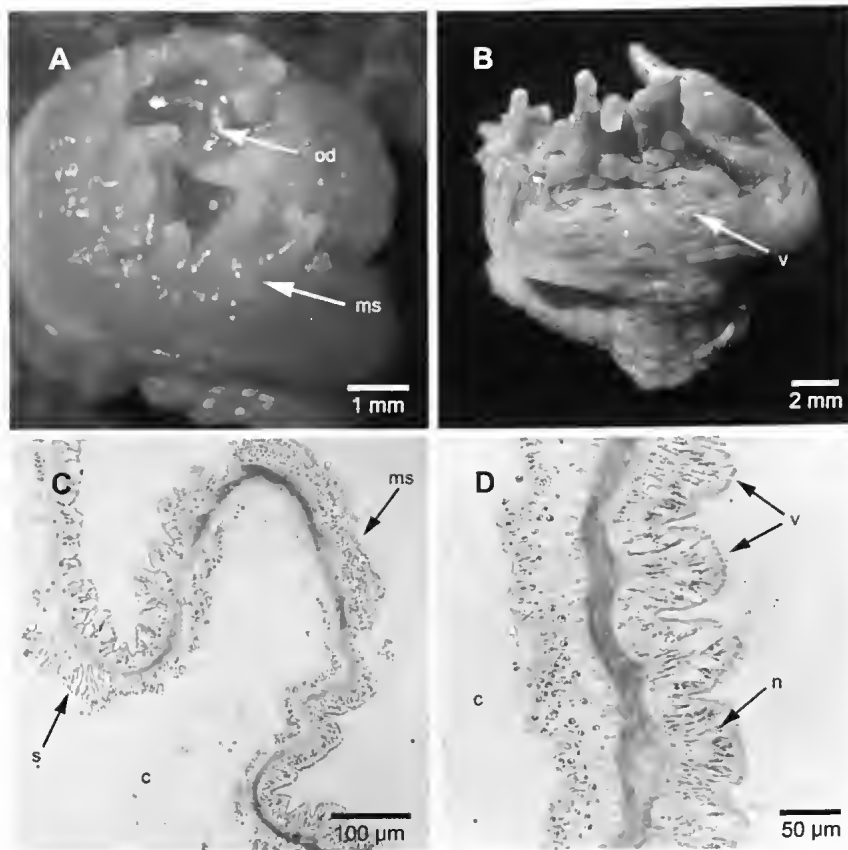
FIG. 10. *Gyractis sesere* from Adam's Beach, North Stradbroke I. Preserved whole animal, MTQ-G59436. **A,** view of oral disc (od) showing marginal spherules (ms). **B,** side view of column showing adhesive verruca (v). **C, D,** longitudinal section through distal column showing: **C,** diffuse endodermal sphincter muscle (s) and marginal spherule (ms); **D,** verrucae (v) with nematocyst (n). (c): coelenteron.

Comments. This species was recorded only outside Moreton Bay proper: specimens were common at all sites dived. It hosts anemonefish (Fautin & Allen 1992). When fish are present, most tentacles are swollen into a terminal or subterminal bulb: bulbs may disappear in anemones lacking fish. Both clonal and solitary forms occur.

Further literature. TAXONOMY & DISTRIBUTION: Dunn (1981); Fautin (1988); Fautin & Allen (1992); Richardson *et al.* (1997). BIOLOGY & ECOLOGY: Dunn (1981, 1985); Fautin (1985, 1986, 1991); Hirose (1985); Fautin & Allen (1992); den Hartog (1997b); Arvedlund *et al.* (1999); Srinivasan *et al.* (1999); Astalhov (2002); Scott & Harrison (2005).

Gyractis Boveri, 1893

Definition. Well-developed pedal disc. Column with longitudinal rows of adhesive verrucae. Marginal spherules well developed, commonly digitate. Endodermal marginal sphincter muscle weak and diffuse, or strong and circumscribed. Tentacles and mesenteries regularly or irregularly arranged. Siphonoglyphs two or more, some supported by directive mesenteries. About same number of mesenteries distally and proximally. Mesenterial retractor and parietobasilar muscles weak to strong, diffuse. Cnidom: spirocysts, basitrichs, microbasic amastigophores, microbasic *p*-mastigophores; in some species heterotrichs occur near the limbus.

Type species. *Gyractis excavata* Boveri, 1893.

Gyractis sesere (Haddon & Shackleton, 1893)
(Fig. 10)

Actinioides sesere Haddon & Shackleton, 1893: 126–127; Haddon, 1898: 428, pl. 22, figs 8, 9, pl. 28, figs 1, 2.
Gyractis excavata Boveri, 1893: 250–251, figs 3, 4, 6.

Gyractis pallida Boveri, 1893: 251–252, figs 1, 2, 5.
Actinioides sultana Carlgren, 1900: 43–44, pl. 1, figs 12, 13.
Actinioides rapanuiensis Carlgren, 1922: 151–153, figs 8, 9, 10.

Material Examined. SYNTYPE: *Actinioides rapanuiensis*, NHMG-848, Easter I. OTHER MATERIAL: *Moreton Bay.* MTQ-G59435, North Stradbroke I., A.-N. Lörz, 2005; MTQ-G59436, 20 spec., Adam's Beach, North Stradbroke I., J. Phillips, 2005.

Appearance. Well developed pedal disc. Column to 8 mm long (preserved specimens), with verrucae in longitudinal rows. Fosse shallow. Sphincter muscle weak, diffuse tending to circumscribed. Tentacles to >100, longitudinal muscles ectodermal; siphonoglyphs weak, not connected to directive mesenteries.

Habitat. Intertidal, in crevices on rocky reef surfaces.

Distribution. Eastern Africa; Gulf of Aden; Singapore; Torres Strait; Western Australia; Queensland; Hawai'i. Type locality: Mabuiag, Torres Strait.

Further literature. TAXONOMY & DISTRIBUTION: Carlgren (1949, 1954); Dunn (1974); Cutress (1977); Cutress & Arneson (1987); Fautin (1988, 2005).

Macrodactyla Haddon, 1898

Definition. Pedal disc distinct, circular, narrower than oral disc. Column with adhesive verrucae distally, without marginal spherules. Fosse absent or deep. Endodermal marginal sphincter muscle restricted, rather weak. Tentacles long and stout, about 48, the inner considerably longer than the outer. Actinopharynx with two siphonoglyphs. Six pairs of complete mesenteries, two of them directives; all fertile; retractor muscles band-like, restricted. Parietobasilar muscles well developed, forming a fold. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species. *Condylactis aspera* Haddon & Shackleton, 1893.

Macrodactyla doreensis (Quoy & Gaimard, 1833) (Fig. 11)

Actinia doreensis Quoy & Gaimard, 1833: 149–150, pl. 12, fig. 7.
Condylactis gelam Haddon & Shackleton, 1893: 123–124.

Material Examined. SYNTYPE: *Condylactis gelam*, UMZ-Co181, 2 spec., Torres Strait. OTHER MATERIAL: *Moreton Bay.* MTQ-G58748, Dunwich, North Stradbroke I., P. Davie, 2005; AM-G16759, North Stradbroke I., E. Pope, 1961; AM-G16979, Dunwich, North Stradbroke I., E. Pope, 1961. *Australia Elsewhere.* MTQ-G59156, Arafura Sea, Nhulunbuy (Gove), NT, B. & B. Koenecke, 2005.

Appearance. Pedal disc circular, buried in sand/mud substrate, not as wide as column. Column to 150 mm long, distal end broadly flared (Fig. 11C); typically grey with splotches of orange or entire column orange with creamy yellow proximal end. Verrucae circular to eye-shaped, non-adhesive, in longitudinal rows, most endocoelic. Fosse pronounced. Oral disc with central, lipped mouth, sometimes on an elevated cone (Fig. 11A, B). Each pointed tentacle grey with pink or mauve tip, may have longitudinal white streak (Fig. 11A); sparse, 50–100 mm long; some with corkscrew form. Tentacles concentrated at margin of oral disc (Fig. 11B), few tentacles scattered on oral disc closer to mouth.
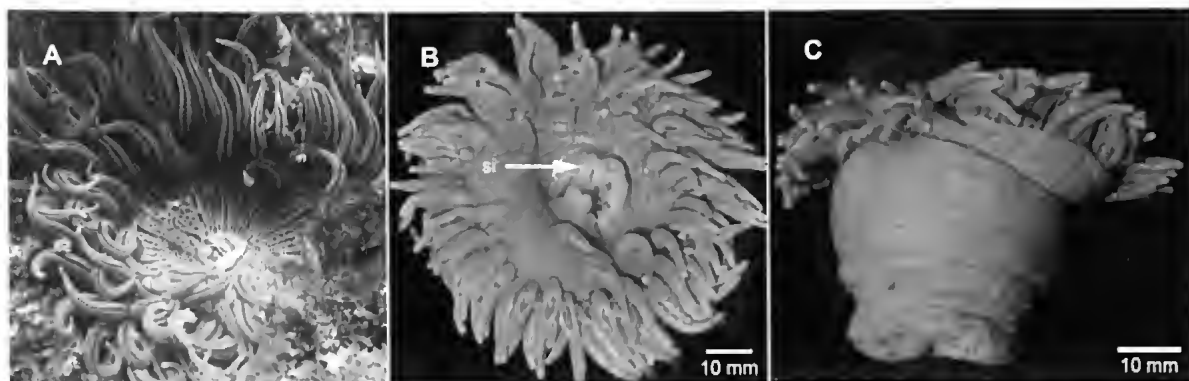
FIG. 11. *Macrodactyla doreensis.* **A**, individual *in situ* on Flat Rock, North Stradbroke I., showing white lips, patterning of oral disc and tentacles, and tentacle-free central area (photograph: J. Hsieu). **B, C**, preserved specimen, MTQ-G58748, from intertidal mudflats, Dunwich, North Stradbroke I.; arrow in B indicates white siphonoglyph (si).

Habitat. Intertidal and subtidal on mud or sand with column partly buried in the substrate.

Distribution. Japan; Papua New Guinea; Hawai'i; northern and eastern Australia, south to Moreton Bay. Type locality: Manokwari [Port Dorey], New Guinea.

Further literature. TAXONOMY & DISTRIBUTION: Moyer (1976); Dunn (1981); Fautin (1988); Fautin & Allen (1992); den Hartog (1997b); Richardson *et al.* (1997). BIOLOGY: Fautin (1991); den Hartog (1997a); Astalhov (2002).

Oulactis Milne Edwards & Haime, 1851

Definition. Pedal disc well developed. Column smooth basally, distally with longitudinal rows of verrucae; verrucae below margin small, frond-like, close-set on lobes. Fosse distinct. Marginal spherules present. Endodermal sphincter muscle diffuse. Tentacles rather short, hexamerously arranged, their longitudinal muscles ectodermal. Two well-developed siphonoglyphs and two pairs of directive mesenteries. Most mesenteries complete and fertile (directives may be sterile); retractor muscles more or less band-like. Cnidom: spirocysts, holotrichs, basitrichs, microbasic *p*-mastigophores.

Type species: *Metridium muscosum* Drayton in Dana, 1846.

Oulactis muscosa (Drayton in Dana, 1846)
(Fig. 12)

Metridium muscosum Drayton in Dana, 1846: 153–154, pl. 5, figs 42, 43.
Oulactis muscosa Milne Edwards & Haime, 1851: 12.
Oulactis plicatus Hutton, 1878: 311–312.

Material Examined. *Moreton Bay.* MTQ-G58750, Frenchman's Beach, DGF, 2005; MTQ-G58756, Cylinder Beach, DGF *et al.*, 2005; QM-G10535, Sandgate, 1951; QM-G31722, Point Lookout, North Stradbroke I., J.N.A. Hooper *et al.*, 2000. *Australia Elsewhere.* AM-G2622, from Straham to Hobart, Tasmania; AM-G10871, Coogee, NSW; AM-G16868, 2 spec., Forster, NSW, 2003; AM-G16961, 2–4 spec., Newport, NSW, 2005; AM-G16974, 3 spec., Tasmania, 1958.

Appearance. Pedal disc broader than length of column, well developed, adhesive. Column to 13 mm long, grey with reddish-brown to dark green spots on verrucae especially near oral end, and brown radial stripes near pedal end. Oral disc dark red, flat, diameter to 10 mm; tentacles concentrated near margin. Tentacle length 3 mm in preservation. In live specimens each tentacle somewhat longer than oral disc diameter, pale brown with grey-striped white base. Acrorhagi prominent; distalmost frond-like verrucae form ruff at margin; sand and shell grit attached to more proximal verrucae. Cnidom: spirocysts, holotrichs, basitrichs, microbasic *p*-mastigophores.

Habitat. Crevices and rock pools on rocky platforms. Base of anemone attached deep in crevice makes collecting difficult.

Distribution. Eastern Australia from southern Queensland to South Australia; New Zealand. Type locality: Illawarra, Wollongong, New South Wales, Australia.

Comments. Two species of *Oulactis* are recognised from Australia (Edgar 1997): *O. muscosa* occurs from the east coast to the Spencer Gulf in South Australia, whereas *O. mcmurrichi* (Lager, 1911) occurs from South Australia westward to Perth, Western Australia. A study is under way to determine whether these species are distinct from one another.

Further literature. TAXONOMY & DISTRIBUTION: Milne Edwards & Haime (1851); Lager (1911); Carlgren (1949, 1950a, b, 1954); Parry (1951); Cutress (1971); Dawson (1992); Edgar (1997); Häussermann (2003). BIOLOGY & ECOLOGY: Hunt & Ayre (1989); Acuña & Zamponi (1999).

ALICIIDAE

Triactis Klunzinger, 1877

Definition. Pedal disc well developed. Column smooth except for central ring of stalked dichotomously ramified outgrowths, which increase in number and degree of branching with age of individual. Hemispheric vesicles containing microbasic and macrobasic amastigophores occur on the stalk near branches, and on the column near oral side of the stalk. Stalk with few, longitudinal, very weak bands of endodermal muscles. No marginal sphincter muscle. Margin tentaculate; tentacles not numerous, hexamerously arranged. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal. Two distinct siphonoglyhs. Six pairs of complete mesenteries and several incomplete; two pairs of directives; retractor muscles weak. Parieto-basilar muscles very weak. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic amastigophores, macrobasic amastigophores.

Type species: *Triactis producta* Klunzinger, 1877.

Triactis producta Klunzinger, 1877
(Fig. 13)

Triactis producta Klunzinger, 1877: 85–86, pl. 6, fig. 8.
Viatrix cincta Haddon & Shackleton, 1893: 117, 127.
Phyllodiscus indicus Stephenson, 1922: 280–281.
Sagartia pugnax Verrill, 1928: 18–19, pls 3B, 4A, fig. 2j.

Material Examined. SYNTYPE: *Sagartia pugnax*, BPBM-D113, Hawai'i. OTHER MATERIAL: *Moreton Bay*. MTQ-G58758, Shark Gutter, M. Preker, 2005. *Australia Elsewhere*. MTQ-G59162, Nhulunbuy (Gove), NT, 2005; QM-G5300, Heron I., Qld.

Appearance. Pedal disc well developed. Column to 60 mm long (6 mm in Moreton Bay specimen), cylindrical; to 8 stalked hemispherical vesicles per branch in Moreton Bay specimen. Tentacles rather short, in three cycles (12+12+24 = 48). Pale brown colour due to endodermal zooxanthellae.

Habitat. Reef surfaces from intertidal to subtidal. Often associated with 'boxer crabs' (*Lybia* species) that grasp these anemones in their specially modified chelae. The Moreton Bay specimen reported here was unattached.

Distribution. Red Sea; tropical Australia; Hawai'i. Type locality: Red Sea.

Further literature. TAXONOMY & DISTRIBUTION: Haddon & Shackleton (1893); Fishelson (1970); Cutress (1977); Cutress & Arneson (1987); England (1987); den Hartog (1997a); Paulay *et al.* (2003). BIOLOGY & ECOLOGY: Karplus *et al.* (1998).
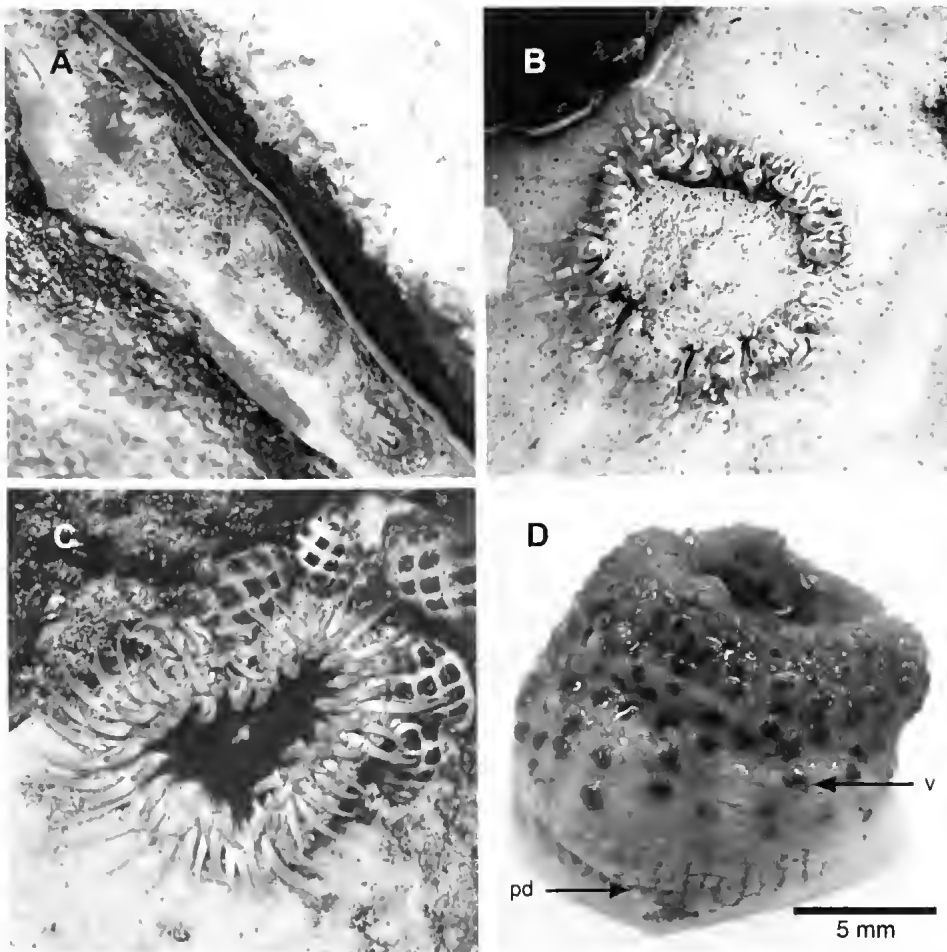
FIG. 12. *Oulactis muscosa*. **A**, specimens in a crevice between two rocks, Cylinder Beach, North Stradbroke I. **B**, individual partly hidden by sand. **C**, exposed individual surrounded by mulberry whelks *Morula marginalba* (photograph: QM). **D**, preserved individual, MTQ-G58750, from Frenchman's Beach, North Stradbroke I., showing broad pedal disc (pd) and column with adhesive verrucae (v).
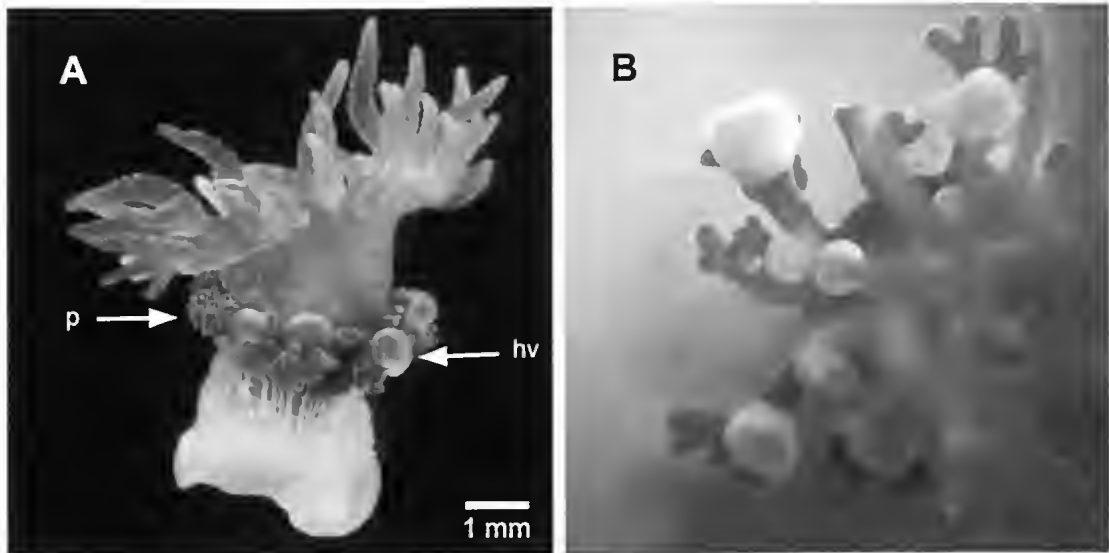
FIG. 13. *Triactis producta*. Individual from Shark Gutter, Flat Rock, North Stradbroke I., MTQ-G58758. **A**, live in laboratory, showing mid-column projections (p) with stalked hemispherical vesicles (hv) (photograph: I. Lawn). **B**, detail of projections.

PHYMANTHIDAE

Heteranthus Klunzinger, 1877

Definition. Pedal disc well developed. Column, apart from most proximal part, with verrucae, which are smaller and more numerous at the margin, and overhang the fosse. Endodermal marginal sphincter muscle weak, circumscribed, forming only a few folds. Marginal tentacles conical, simple, arranged in cycles; discal tentacles much shorter and papilliform, in radial rows. Two well-developed siphonoglyphs. Fairly numerous perfect pairs of mesenteries, two pairs of directives; retractor muscles diffuse, well developed. Parietobasilar muscles weak to fairly strong. Distribution of gametogenic tissue unknown. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Heteranthus verruculatus* Klunzinger, 1877.

Heteranthus verruculatus Klunzinger, 1877
(Fig. 14)

Heteranthus verruculatus Klunzinger, 1877: 84, pl. 5, fig. 9.

Material Examined. SYNTYPES: MNB-1852, SMNH-1861, Red Sea. OTHER MATERIAL: *Moreton Bay*. MTQ-G59391, Bird I., A.-N. Lörz & DGF, 2005; MTQ-G59392, Shag Rock, G. Carini & I. Fellegara, 2005; MTQ- G59967, Shag Rock, M. Preker, 2005; MTQ-G59968, Moreton Bay, 2005. *Australia Elsewhere*. MTQ-G59393, Mystic Sands, north of Townsville, Qld, ALC & C. Bartlett, 2005.

Appearance. Column to 9 mm length, 11 mm diameter; pale yellowish-green proximally, greenish–brown distally (owing to zooxanthellae); verrucae bright green with central white spot, becoming tentacle-like at margin (Fig. 14A). Oral disc dark greenish-brown to sepia, with variable amounts of opaque white. Marginal tentacles smooth, pointed, inner longer than outer, pale greenish-brown with no patterning or with dense pattern of opaque white flecks and circular spots; discal tentacles papilliform, inconspicuous, same colour as oral disc .

Habitat. In sand or on rocks, often part-hidden by sand, from intertidal to subtidal, on coral reefs and rock platforms.

Distribution. Red Sea; Western Australia; Queensland; Hawai'i. Type locality: Red Sea.

Comments. This species seems to be common in Queensland: it occurs both within and outside Moreton Bay; dense aggregations occur in Townsville; and Carlgren (1950c) recorded it (with some hesitation) from the Great Barrier Reef.

Further literature. TAXONOMY & DISTRIBUTION: Haddon (1898); Carlgren (1950c); Cutress (1977); den Hartog (1997a). BIOLOGY: Stephenson (1922).
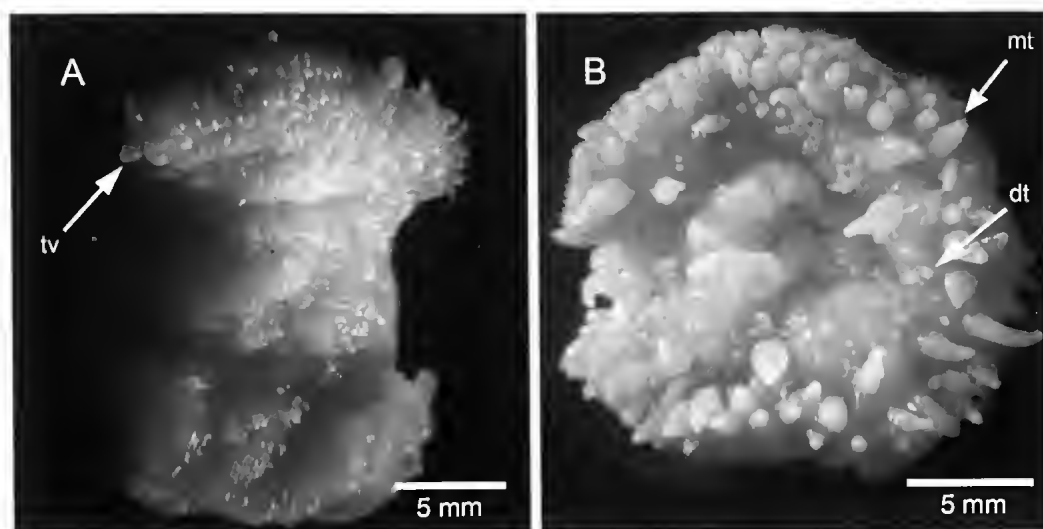
FIG. 14. *Heteranthus verruculatus* from Shag Rock, North Stradbroke I., preserved specimen, MTQ-G59392. **A**, side view of column indicating tentacle-like verruca (tv) at margin. **B**, oral disc, showing pointed marginal tentacles (mt) and papilliform discal tentacles (dt).

STICHODACTYLIDAE

Stichodactyla Brandt, 1835

Definition. Pedal disc well developed, adherent. Flat, undulating, and broad oral disc covered with many short tentacles; endocoelic tentacles radially arrayed, mostly two or more abreast, to five at margin; rows communicating with successively higher order endocoels shorter, more marginal; in most species all tentacles alike, but single exocoelic ones may be more robust. Column generally broader than tall, flared part verrucose. Fosse absent to shallow. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Stichodactyla mertensii* Brandt, 1835.

Stichodactyla haddoni (Saville-Kent, 1893)
(Fig. 15)

Discosoma Haddoni Saville-Kent, 1893: 32–33, chromo pl. 2, pl. 21.

Material Examined. *Moreton Bay*. QM-G10528, Dunwich, North Stradbroke I., 1951; QM-G309200, Flinders Reef; QM-G317137, Raby Bay, Cleveland, S.D. Cook *et al.*, 2000; QM-G327091, Dunwich, North Stradbroke I., J.N.A. Hooper *et al.*, 2000; QM-G327354, Wellington Point, S.E. List-Armitage, ALC & C.J. Bartlett. *Australia Elsewhere*. MTQ-G55351, Pallarenda, Townsville, Qld, ALC & PRM, 2005; NTM-C3240, Trepang Bay, van Dieman Gulf, NT, 1981; NTM-C10010–13, Ashmore Reef, WA, 1986.

Appearance. Well-developed pedal disc. Oral disc to 500 mm diameter, undulating, green, brown, or blue; densely covered with short tentacles (a few mm long, about 1 mm diameter) although area around mouth typically tentacle-free. Tentacles sticky to touch; basal portion of tentacle of uniform diameter, upper portion bluntly pointed to slightly bulbed; most single exocoelic tentacles white, about 3 mm diameter. Column white, yellow, or light green, widening gradually from pedal disc to flared upper column bearing small non-adhesive verrucae. Fosse shallow.

Habitat. Intertidal to subtidal sand or mud flats.

Distribution. Red Sea; eastern Africa; Singapore; northern and eastern Australia south to Moreton Bay; Japan; New Caledonia. Type locality: Flat Top Island, Great Barrier Reef, off Mackay, Qld, Australia.

Comments. This is the largest sea anemone in the Moreton Bay region. It is known as a 'carpet anemone' in the aquarium trade.

Further literature. TAXONOMY & DISTRIBUTION: Carlgren (1950c); Dunn (1981, 1985); Fautin (1988); den Hartog & Vennam (1993); Richardson *et al.* (1997); den Hartog (1997a, b); Uchida & Soyama (2001); Astalhov (2002); Paulay *et al.* (2003). BIOLOGY & ECOLOGY: Hadley (1973); Dunn (1981); Hirose (1985); Fautin (1991); Khan *et al.* (2003, 2004).
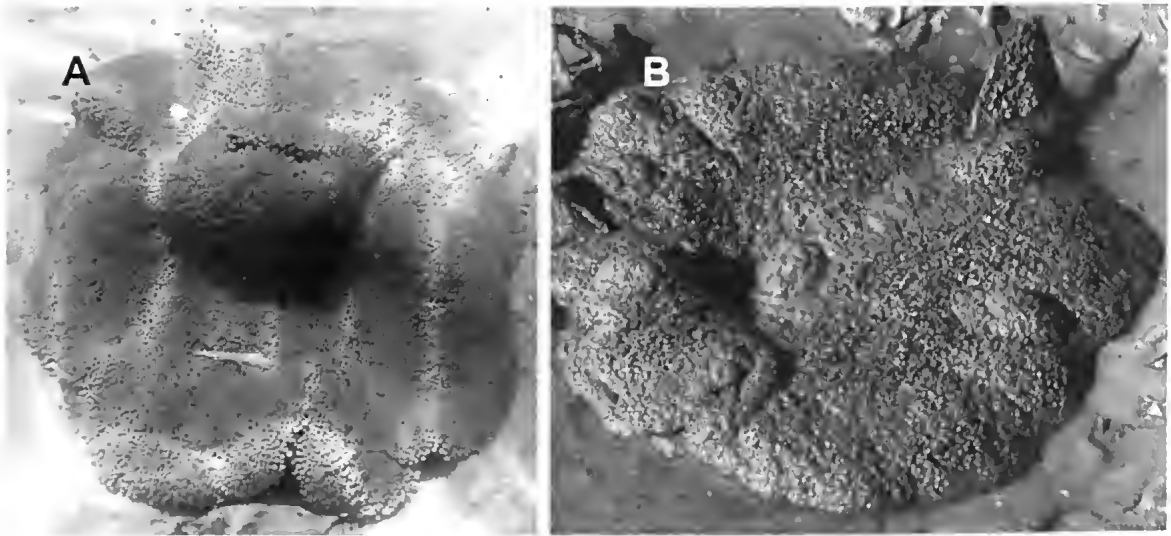
FIG. 15. *Stichodactyla haddoni*. **A,** individual from Days Gutter, off Moreton I., showing large oral disc with evenly distributed short tentacles. **B,** animal on mud flat exposed at very low tide (photograph: QM).

Stichodactyla tapetum (Hemprich & Ehrenberg in Ehrenberg, 1834)
(Fig. 16)

Actinia (Isacmaea) Tapetum Hemprich & Ehrenberg in Ehrenberg, 1834: 256.
Homactis rupicola Verrill, 1869b: 71–72.
Discosoma ambonensis Kwietniewski, 1898: 387, 410–412, 413, pl. 29, figs 49–51.
Stoichactis laevis Lager, 1911: 240–241, figs 16, 17.
Stoichactis australis Lager, 1911: 241–243, fig. 18.

Material Examined. HOLOTYPES: *Stoichactis australis*, ZMH-5332; *Stoichactis laevis*, ZMH-5337; *Homactis rupicola*, YPM-6854. SYNTYPES: *Actinia tapetum*, MNB-162, 5 spec., MNB-163 3 spec.; SMNH-1157. *Discosoma ambonensis*, SMNH-5580. OTHER MATERIAL: *Moreton Bay*. AM-G4085, 3 spec., North Stradbroke I., Qld; AM-G16071, 3 spec., Dunwich, North Stradbroke I., Qld, 1961; AM-G16072, 3 spec., Dunwich, North Stradbroke I., Qld, 1961. *Australia Elsewhere*. QM-G16913, Northwest I., Capricorn Group, Great Barrier Reef, Qld, 1931.

Appearance. Pedal disc to 30 mm diameter; oral disc to 100 mm diameter, typically no greater than 40 mm. Column length typically about one half pedal disc diameter, but may be taller. Tentacles very short, 0.25–0.5 mm diameter; bulbous; densely packed, may be arrayed in fields on entire disc. Two symmetrical siphonoglyphs.

Habitat. In rock crevices on fringing coral reefs; on mud and sand flats.

Distribution. Red Sea; Hong Kong; China; Taiwan; Indonesia; Singapore; tropical eastern and western Australia. Type locality: Red Sea.

Comments. This species does not host anemonefish. During the Workshop this species was not observed inside the Bay, but specimens in the Australian Museum were collected from Dunwich, within Moreton Bay, in 1961.

Further literature. TAXONOMY & DISTRIBUTION: Dunn (1981); den Hartog (1997a); Uchida & Soyama (2001); Song & Cha (2004).

Heteractis Milne Edwards, 1857

Definition. Pedal disc well developed, adherent, slightly wider than lower column, narrower than oral disc. Column length of some equal to oral disc width, of some equal to pedal disc width. Proximal column smooth, distally with inconspicuous to prominent verrucae. Fosse absent to deep. Oral disc hardly retractile, flat to shallowly undulating. Tentacles on one individual all alike, sinuous to digitiform; one species has swellings on lateral and oral surfaces. Usually more than one tentacle per endocoel. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Actinia aurora* Quoy & Gaimard, 1833.

Heteractis malu (Haddon & Shackleton, 1893)
(Fig. 17)

Discosoma Malu Haddon & Shackleton, 1893: 120.
Stichodactis papillosa Kwietniewski, 1898: 415–417, pl. 28, figs 41–45.
Antheopsis concinnata Lager, 1911: 244–245, fig. 20.
Stichodactis glandulosa Lager, 1911: 246–247, fig. 21.
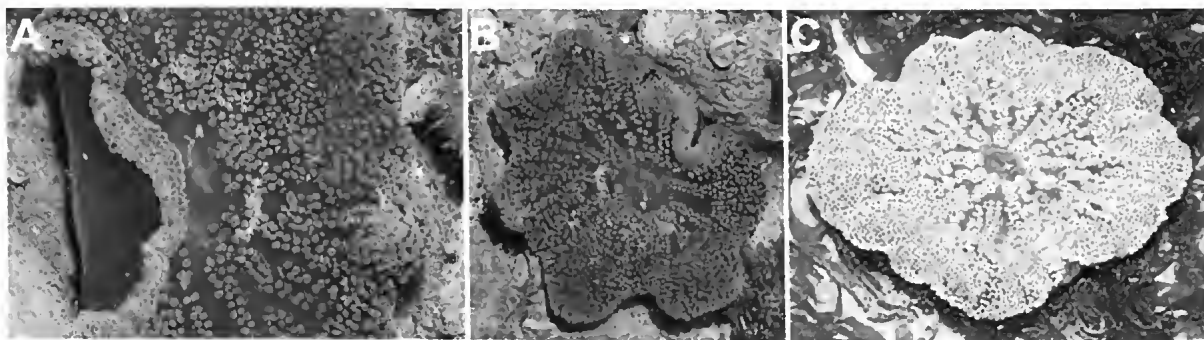
FIG. 16. *Stichodactyla tapetum*. **A-C** (photographed in Singapore waters, but typical of those found in Moreton Bay. (photographs: Ria Tan, wildsingapore.com)

Stichodactis Kwietniewskii Lager, 1911: 247–248, fig. 22.

Macranthea cookei Verrill, 1928: 12–13, pl. 3, fig. A.

Material Examined. HOLOTYPES: *Stichodactis kwietniewskii*, ZMH-5342, Barrow I., WA. *Discosoma malu*, UMZ-Co206, Torres Strait. *Stichodactis glandulosa*, SMNH-667, Broome, WA. SYNTYPE: *Antheopsis concinnata*, ZMH-5318, Shark Bay, WA. OTHER MATERIAL: *Moreton Bay*. MTQ-G58749, Shag Rock, MM & CCW, 2005; MTQ-G59738, Shag Rock, G. Carini & I. Fellegara, 2005; MTQ-G59971, Shag Rock, M. Preker, 2005; MTQ-G59970, Flat Rock, I. Fellegara, 2005; MTQ-G59973, Henderson Rock, A.-N. Lörz, 2005; MTQ-G59972, Manta Ray Bombies, North Stradbroke I., G. Carini, 2005; QM-G309201, Days Gutter off Moreton I., AIMS/NCI, 1988. *Australia Elsewhere*. QM-G309350, Cockburn Sound, WA; WAM-23-76, Shark Bay, WA; WAM-26-76, Ningaloo, WA.

Appearance. Pedal disc thin-walled, colourless, mesenterial insertions seen as light radial lines. Column to 200 mm long; diameter increases distally; colour cream; verrucae adhesive. Fosse shallow. Oral disc brown, purple, or green, with white markings; flat in expansion, to 200 mm diameter, but smaller in Moreton Bay specimens. Mouth 10–20 mm long, slit-like to circular. Tentacles uniform size, evenly tapered from base or slightly wider in central region, to 40 mm long and 3 mm diameter when expanded; lower portion same colour as oral disc, upper portion light in some individuals, ringed with several broad white bands in others, or white in centre third and green at end; tip may be mauve or red; grey-green in contraction due to endodermal zooxanthellae.

Habitat. Reef environments, commonly burrowed into soft sediment.

Distribution. Indonesia; Papua New Guinea; Japan; Hawai'i; Australia from Broome to Point Peron in Western Australia, Torres Strait to Moreton Bay in Queensland. Type locality: Torres Strait, Australia.

Further literature. TAXONOMY & DISTRIBUTION: Dunn (1981); Fautin (1988); Fautin & Allen (1992); Uchida & Soyama (2001). BIOLOGY & ECOLOGY: Dunn (1981); Fautin (1991); den Hartog (1997b); Arvedlund *et al.* (1999); Astalhov (2002).

Heteractis crispa (Hemprich & Ehrenberg in Ehrenberg, 1834)
(Fig. 18)

Actinia crispa Hemprich & Ehrenberg in Ehrenberg, 1834: 260, pl. 8, fig. 1.

Actinia paumotensis Couthouy in Dana, 1846: 141, pl. 3, fig. 25.

Discosoma macrodactylum Haddon & Shackleton, 1893: 117, 120–121.

Radianthus Kükenthali Kwietniewski, 1896: 389–390.

Discosoma tuberculata Kwietniewski, 1898: 387, 412–413, pl. 28, figs 46–48.

Radianthus lobatus Kwietniewski, 1898: 387, 414–415, pl. 28, figs 38–40.

Material Examined. HOLOTYPE: *Radianthus lobatus*, PMJ-Coel69. LECTOTYPE: *Actinia paumotensis*, USNM-1690. SYNTYPES: *Discosoma macrodactylum*, UMZ [no catalogue number], 3 spec., Torres Strait. *Discosoma tuberculata*, PMJ-Coel65, 3 spec., SMNH-5881, Ambon. *Radianthus kükenthali*, SMF-101; SMNH-5686; MNB-3579; PMJ-Coel67; PMJ-Coel68. OTHER MATERIAL: *Moreton Bay*. MTQ-G59969, Flat Rock, M. Preker, 2005. *Australia Elsewhere*. QM- G309064, Big Broadhurst Reef, off Townsville, Qld; CAS-010397, Heron I., Qld.

Appearance. Column widens gradually from pedal disc, flared at oral end; texture leathery, grey, each prominent verruca with raised rim. Fosse shallow or absent. Expanded specimens about as long as oral disc diameter. Oral disc flat, to 500 mm diameter. Tentacles sinuous,
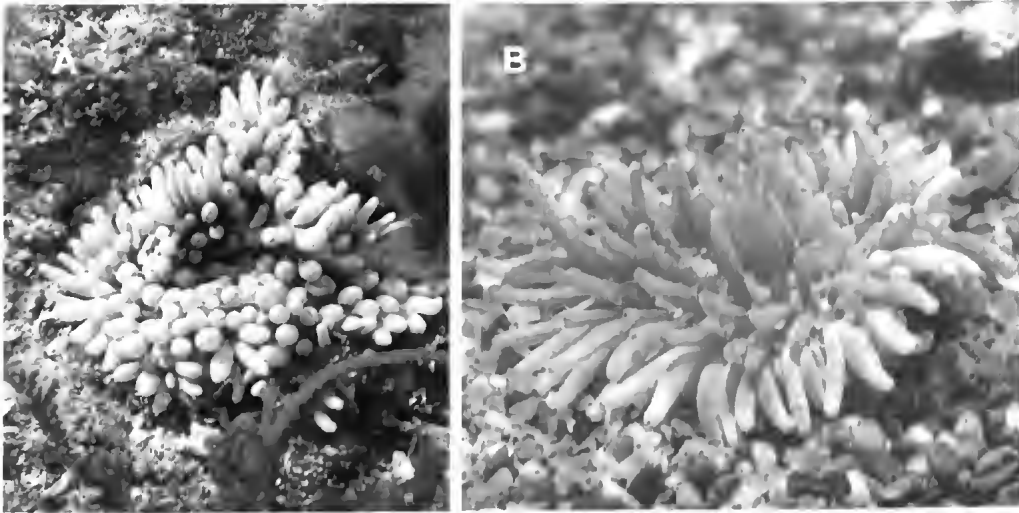
FIG. 17. *Heteractis malu*. **A,** individual *in situ* at Flat Rock, North Stradbroke I. (photograph: J. Hsieu). **B,** individual from Shag Rock, North Stradbroke I., MTQ-G58749, in aquarium, showing sturdy cylindrical tentacles arranged most densely around margin (photograph: G. Cranitch).
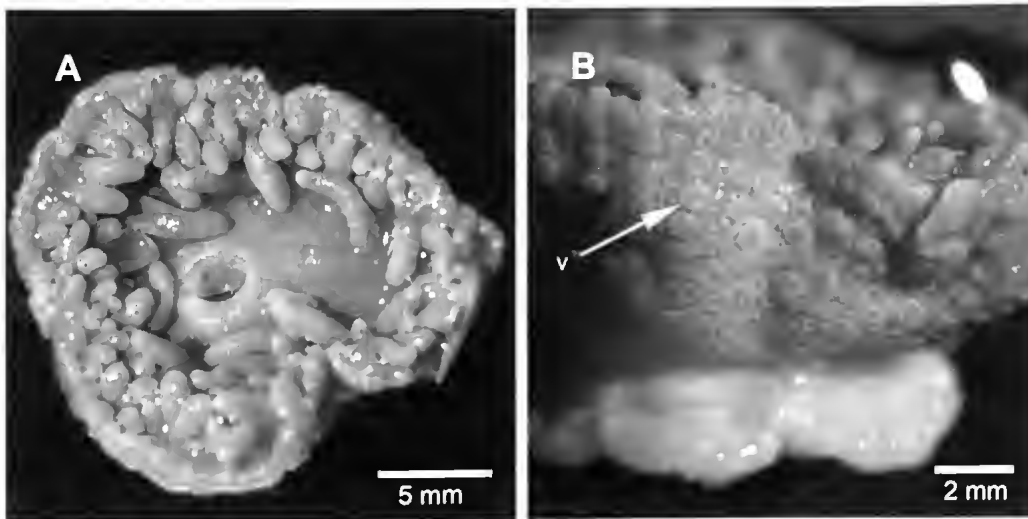
FIG. 18. *Heteractis crispa* from Flat Rock, North Stradbroke I., preserved juvenile specimen, MTQ-G59969. **A,** oral disc, showing tentacles concentrated around outer edge; **B,** side view of column, showing flaring upper section with conspicuous verrucae (v).

tapering to pointed tip; length generally a quarter to a third oral disc diameter, inner may be longer than outer; same colour as oral disc, some with pink, mauve, or blue tip. Mouth elongate. Actinopharynx white to yellow with two deep white siphonoglyphs. Base adherent, generally flat, rarely exceeding diameter of lower column.

Habitat. Reef environment. May be attached to branching coral, but column commonly buried in sediment with oral disc at surface.

Distribution. Red Sea; Seychelles; Micronesia; Melanesia; Japan; Australia northern and eastern coasts; French Polynesia. Type locality: Red Sea.

Comments. The leathery texture of the column is one of the distinguishing features of this species.

Further literature. TAXONOMY & DISTRIBUTION: Haddon & Shackleton (1893); Dunn (1981, 1985); Hirose (1985); Fautin (1988); Fautin & Allen (1992); den Hartog (1997a, b); Richardson *et al.* (1997); Paulay *et al.* (2003). BIOLOGY: Dunn (1981); Hirose (1985); Fautin (1991); Astalhov (2002); Hermansen *et al.* (2005); Scott & Harrison (2005).

DIADUMENIDAE

Diadumene Stephenson, 1920

Definition. Pedal disc well developed. Smooth column divisible into scapus and capitulum, separated by collar; scapus with cinclides. Margin of capitulum tentaculate. No distinct marginal sphincter muscle. Tentacles long, numerous, more or less regularly arranged, imperfectly or not at all retractile; some or all inner tentacles may form catch-tentacles; some outer tentacles with macrobasic amastigophores. Six or a few more perfect pairs of mesenteries; mesenteries more numerous distally than proximally; retractor muscles diffuse, more or less restricted. Perfect mesenteries and the stronger imperfect ones fertile. Parietobasilar and basilar muscles weak. Acontia well developed, with basitrichs and microbasic *p*-mastigophores. Cnidom: spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores, microbasic amastigophores, macrobasic amastigophores.

Type species: *Sagartia schilleriana* Stoliczka, 1869.

Diadumene sp.
(Fig. 19)

Material Examined. MTQ-G59437, 15 spec., Frenchman's Beach, North Stradbroke I., Moreton Bay, J. Phillips, 2005.

Appearance. Pedal disc diameter 1.2–2.8 mm. Column 1.0–4.4 mm long and 1.0–1.4 mm diameter, pale brown in life. Oral disc diameter 0.8–1.8 mm, darker brown centrally. Tentacles number 44–58; one specimen had a catch tentacle.

Habitat. Underside of rocks in the intertidal zone; one attached to algal frond.

HORMATHIIDAE

Calliactis Verrill, 1869

Definition. Pedal disc well developed. Column smooth, not differentiated or only slightly differentiated into scapus (often with a weak cuticle) and scapulus, often thick; some proximal cinclides do not pierce body wall. Radial muscles of oral disc more or less embedded in the mesogloea. Marginal sphincter muscle strong. Tentacles rather short, conical; more numerous than mesenteries at the base; longitudinal muscles ectodermal. Two broad siphonoglyphs. Six pairs of complete and sterile mesenteries, two pairs of directives; retractor muscles fairly weak, diffuse.

Parietobasilar and basilar muscles weak or rather well developed. Often commensal with hermit crabs. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: *Actinia decorata* Couthoy in Dana, 1846.

Calliactis polypus (Forsskål, 1775)
(Fig. 20)

Priapus polypus Forsskål, 1775: 102.
Actinia decorata Couthoy in Dana, 1846: 139–140, pl. 3, fig. 24.
Adamsia miriam Haddon & Shackleton, 1893: 117, 130–131.
Calliactis armillatas Verrill, 1928: 20–21, pl. 4B.
Calliactis valdiviae Carlgren, 1949: 97.

Material Examined. SYNTYPES: *Calliactis armillatas*, BPBM-D295, D299, D114, Hawai'i. OTHER MATERIAL: *Moreton Bay*. MTQ-G58757, Henderson Rock, C. Buxton & A.-N. Lörz, 2005.

Appearance. Pedal disc follows contour of gastropod shell to which it is attached; to 50 mm diameter. Column 7–14 mm long, maroon, divided into very short smooth scapulus and thicker-walled scapus; small tubercles near distal end; mesenterial insertions visible through column near limbus. Perforate cinclides on prominent white tubercles arranged in a single circle above base. Thin cuticle present, especially near base. Tentacles numerous, smooth, conical, inner longer than outer; occupy marginal third of oral disc. Oral disc flat, circular, diameter 7–20 mm; central mouth with two prominent siphonoglyphs.

Habitat. Attached to shell of hermit crab; may be more than one anemone per shell.

Distribution. Red Sea; Indian Ocean; tropical Pacific Ocean. Type locality: Ghomfodam, Red Sea.

Comments. Specimens in the Australian Museum not identified to species may belong to this species. England (1971) synonymised many species from throughout the Indo-Pacific because of considerable morphological overlap among them, but it is likely there is more than one species (Fautin *et al.*, 2007a).

Further literature. TAXONOMY & DISTRIBUTION: Carlgren (1938, 1950c); England (1971); Cutress (1977); Cutress & Arneson (1987); Pei (1996); den Hartog (1997a); Paulay *et al.* (2003). BIOLOGY: Reimer (1973).
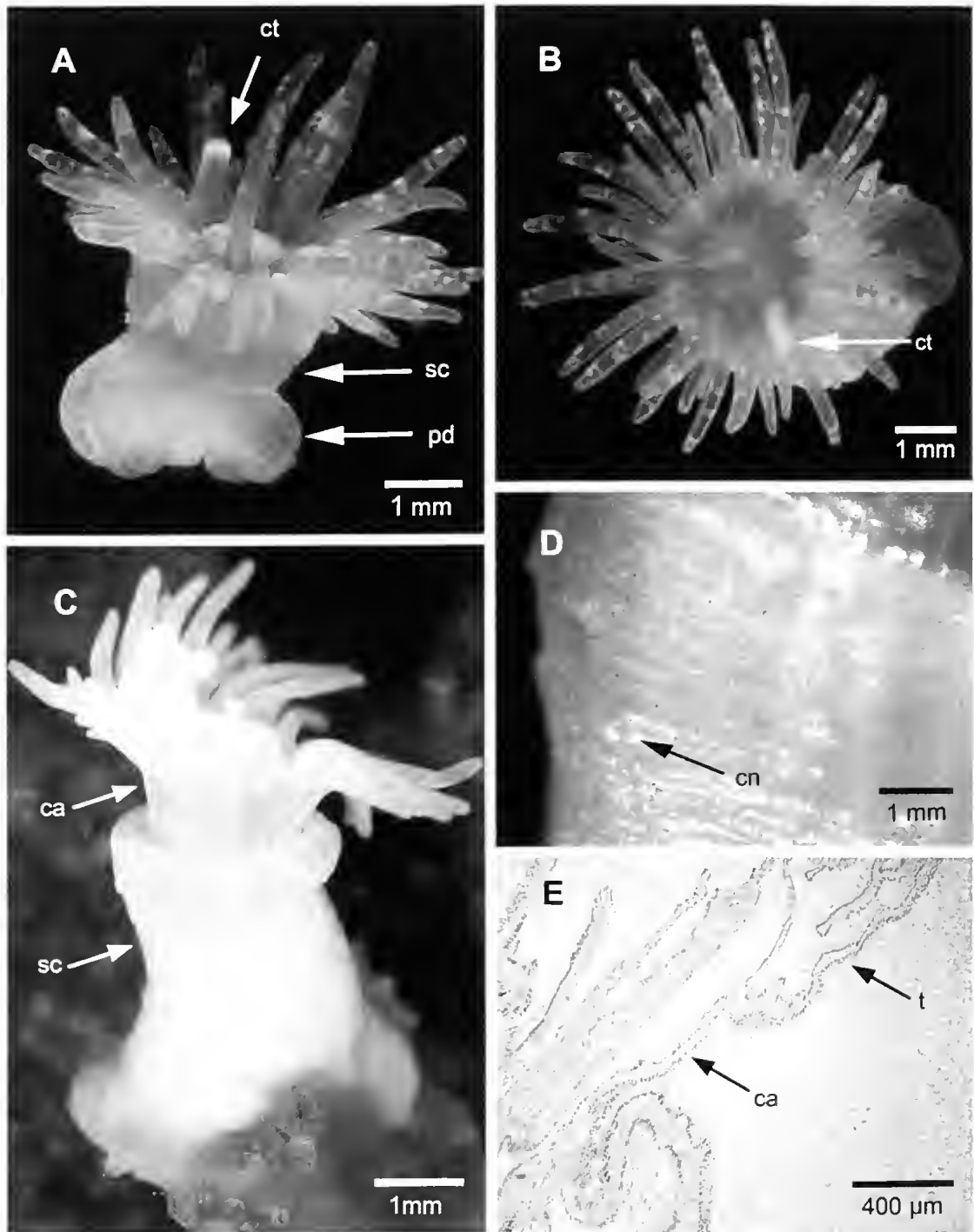
FIG. 19. *Diadumene* sp. from Frenchman's Beach, North Stradbroke I., MTQ-G59437. A-D whole specimen in the laboratory. **A**, showing pedal disc (pd) and scapus (sc) section of column without projections, and blunt catch tentacle (ct) among regular tentacles. **B**, oral disc showing the catch tentacle, which is opaque. **C**, specimen attached to algae, showing scapus (sc) and capitulum (ca) separated by collar. **D**, close-up of scapus at collar showing cinclide (cn). **E**, longitudinal section showing collar region, capitulum (ca), and tentacles (t).
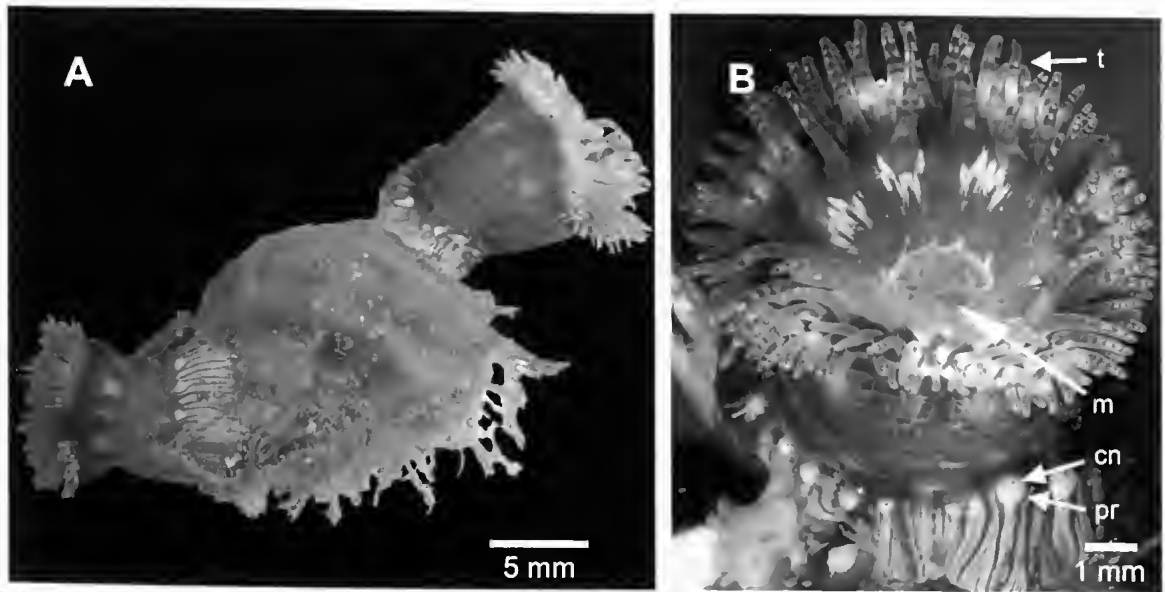
FIG. 20. *Calliactis polypus* from Henderson Rock, MTQ-G58757. **A**, two specimens on gastropod shell. **B**, detail of larger specimen, showing cinclides (cn) on white protuberances (pr), tentacles (t) and central mouth (m) (photograph: I. Lawn).

SAGARTIIDAE

Verrillactis England, 1971

Definition. Pedal disc well developed, adhesive. Column smooth or with ectodermal invaginations that do not pierce column wall; divisible into scapus and scapulus. Mesenteries arranged hexamerously or irregularly; number at base about twice that at margin; 6–12 pairs complete and sterile. One or two siphonoglyphs; may not be supported by directives. Mesogloeal marginal sphincter muscle strong. Inner tentacles longer than outer; some form catch tentacles bearing large holotrichs. Acontia with basitrichs and microbasic amastigophores. Symbiotic with hermit crabs, which are often associated also with *Calliactis polypus*. Cnidom: spirocysts, basitrichs, holotrichs, microbasic amastigophores, microbasic *p*-mastigophores.

Type species: *Sagartia paguri* Verrill, 1869.

Verrillactis paguri (Verrill, 1869)
(Fig. 21)

Sagartia Paguri Verrill, 1869b: 57.

Material Examined. *Moreton Bay*. MTQ-G59434, Henderson Rock, C. Buxton & A.-N. Lörz, 2005.

Appearance. Pedal disc 20 mm x 18 mm, adherent to hermit crab shell. Column white; 3 mm long. Marginal sphincter muscle almost completely fills margin, tapers from ectodermal side proximally. Tentacles conical, smooth, inner longer and thicker than outer; no catch tentacles on Moreton Bay specimens.

Habitat. Lives along aperture of gastropod shell inhabited by hermit crab.

Distribution. Maldives; Taiwan Strait; Korea; Micronesia; eastern Australia; French Polynesia. Type locality: Taiwan Strait, Taiwan.

Comments. Moreton Bay specimens were attached to a shell inhabited by a hermit crab and to which specimens of *Calliactis polypus* were attached also; anemones of the two species occupied different parts of the shell.

Further literature. TAXONOMY & DISTRIBUTION: Verrill (1869b); McMurrich (1903); Carlgren (1949); England (1971, 1987); Cutress & Arneson (1987); Song (1992, 2000); den Hartog (1997a); Song & Lee (1998); Cha & Song (2001); Uchida & Soyama (2001).

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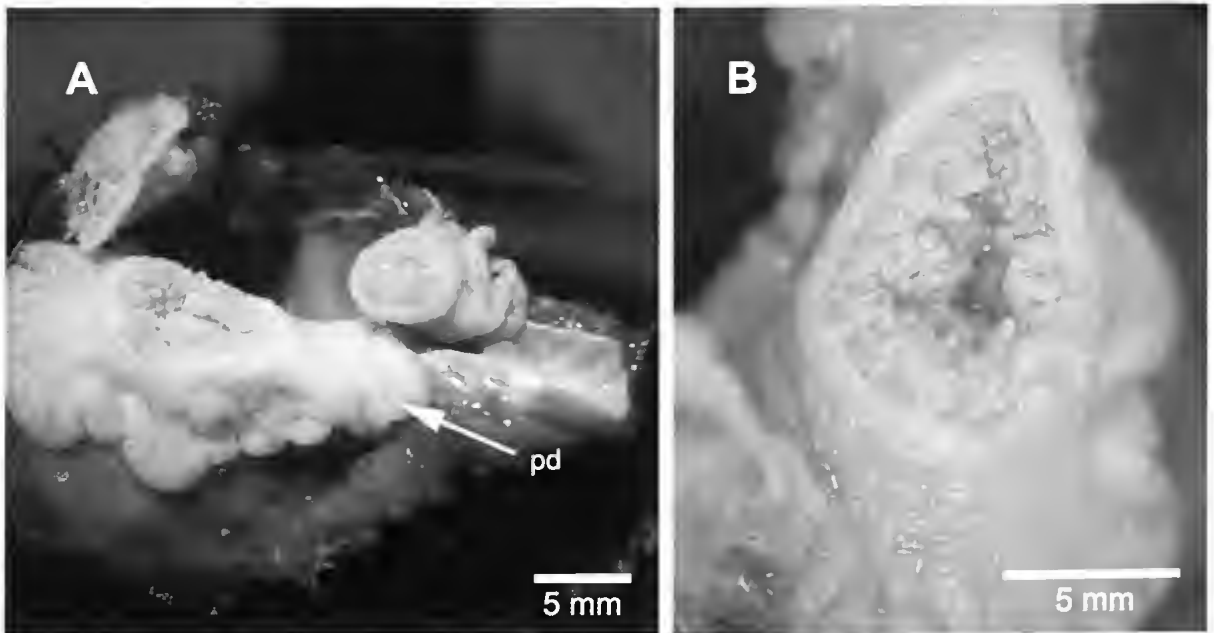
FIG. 21. *Verrillactis paguri* from Henderson Rock, MTQ-G59434. **A**, three specimens on gastropod shell occupied by hermit crab. Note expanded pedal disc (pd). **B**, oral disc and margin of largest specimen.

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A preliminary investigation of the utility of ribosomal genes for species identification of Sea Anemones (Cnidaria: Actiniaria)

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ABSTRACT

The utility of the ribosomal DNA gene complex for species identification of Actiniaria was examined. The use of universal ribosomal PCR primers is problematic in this group due to the presence of algal symbionts. Universal primers were initially used to amplify a region containing partial 18S, complete ITS, 5.8S, ITS2, and partial 28S sequences from six sea anemone species. The development of two sea anemone specific primers for this region was necessary to avoid amplification of algal symbionts for a number of species. Complete sequences of the 18S–28S fragment were obtained from three species, ?*Anemonia* sp. (724 bp), *Heteractis malu* (670 bp) and *Stichodactyla haddoni* (734 bp); partial or non-overlapping sequences were obtained from *Entacmaea quadricolor* (480bp from 18S), *Macrodactyla doreensis* (523 bp: 300bp from 18S and 223bp from 28S) and *Oulactis muscosa* (556bp: 285bp from 18s and 271bp from 28S). Average sequence divergence among sea anemone species was approx. 24% indicating that this region may indeed be useful for species identification. However, unexpectedly low divergence recorded between two species in different genera, neither of which could be verified by histology due to specimen unavailability, indicated that traditional histological methods are still needed to confirm identification and certainly until such time that an rDNA database of sea anemone tissue has been established. ❑ *ribosomal DNA; sea anemone specific primers; universal primers*

In February 2005, the Australian Marine Sciences Association, SEQ Branch, hosted the Thirteenth International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. Fieldwork was conducted over a period of three weeks and occurred in a variety of environments including off-shore reefs, small islands accessible only at low tide, piers, estuarine mouths and mud flats. A taxonomic paper documenting the species found is presented by Fautin *et al.* (2008, this volume). Of the more than 20 species that are now known from More-ton Bay, we obtained tissue from the following six species and genera of anemones to assess the usefulness of DNA in identification, and the potential for understanding phylogenetic relationships: ?*Anemonia* sp., *Heteractis malu*, *Stichodactyla haddoni*, *Entacmaea quadricolor*, *Macrodactyla doreensis* and *Oulactis muscosa.*

Species identification of sea anemones (Anthozoa: Actiniaria) can be difficult, especially in the field. The taxonomic key currently utilised, designed by Oskar Carlgren (1949), is based mainly on histological differences and therefore requires

A) 18S rDNA 3' end

18S rDNA

—— Seaanem18 ——

```
                10         20         30         40         50         60         70         80         90        100]
H. magnifica 1     ------AAT GGTTTAGTGA GGACTCCTGA TTGGGCGCGC CGCCCCGGCA ACGGAGCAGT GGACTTGCCG AAAAGTTGTT CAAACTTGAT CATTTAGAGG
S. haddoni         CCGATTG... .......... .......... .......... .......... .......... ..CC.... . .......... .......... ..........
E. quadricolor     CCGATTG... .......... .......... ..A...... . .......... ..G....... .......... .......... .......... ..........
O. muscosa         CCGATTG... .......... .......... ..A...... . ...c...... .......... .......... .......... .......... ..........
?Anemonia sp.      CCGATTG... .......... .......... .......... .......... ..G....... .......... .......... .......... ..........
Zooxan M. doreensis ----TG.G. .A.CCG.... AT.A...G. . C..A...A.T GCT.AGTTC TG.AC.TT.C .......T.. ...G...... .TCA TG...C.T. . ...C.....
Zooxan H. malu     CCGATTG.G. .A.CCG.... AT.A.T.G. . C..A...A.T GCT.AGTTC TG.AC.TT.C .......T.. ...G...... .TCA TG...C.T. . ...C.....
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ITS 1 →

18S rDNA

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                110        120        130        140        150        160        170        180        190        200]
H. magnifica 1     AAGTAAAAGT CGTAACAAGG TTTCCGTAGG TGAACCTGCG GAAGGATCAT TACCGATCAG CCAAGTCGTT AACTCGACAA CACACCGCGA ACCGTCCCCG
S. haddoni         .......... .......... .......... .......... .......... .......... ..........C .......... .......... ..........
E. quadricolor     .......... .......... .......... .......... .......... ..........GT T.G..GACCG CCACA.TTCT .T.G.AC..C GAACCGTA..
O. muscosa         .......... .......... .......... .......... .......... ..........C GTTCTA.ACG T.GGAC..CG AgA...TAT GGA.AG----
?Anemonia sp.      .......... .......... .......... .......... .......... ..........GA GTTCT..T.G G.ACACCGCG -.A...TAT GGACAG--
Zooxan M. doreensis ..G.G..... .......... .......... .......... .......... -.GC.CTGA TTC.A..T.G .CTA.TG.. .TTTGGCT.T GAG.GATG.T
Zooxan H. malu     ..G.G..... .......... .......... .......... .......... -.GC.CTGA TTC.A.TT.G .CTA..TG. .TTTGGCT.T GAG.GATG.T
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B) 28S rDNA 5' end

ITS 2

28S rDNA

—— Seaanem28 ——

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                10         20         30         40         50         60         70         80         90        100
H. magnifica 1     GCACGGCGTT GGACCGGACG GACG----GT GGTTCGG--- -CCCTATCTT TCCA-TCTTG ACCTCAGATC AGGCGGAGACT ACCCGCTGAA TTTA------
S. haddoni         .......... ...C...... .......... .......... ...G...... .......... .......... .......... .......... .......----
O. muscosa         AGG.CT.TGC T.G.-..... TGCGGAC.. .......CAG C...GC.A . .TTC...... ....T..... .......... .......... ....AGCATA
?Anemonia sp.      AGG..C..GC C.GT-.... .C.CCGT-.C ...C.TCGG- ---CCYT.C .TA.C..... .......... .......... .......... .......----
Zooxan M. doreensis .TTTTA.T.G A.TGAC.CT. CT.ATGCTTG CAAC..CTGG GATGC.GG.G CATGCCTC.A G.A.G.AG.. ..A.A..TGA .......----
```

FIG. 1: Location of sea anemone specific primers Seaanem18S and Seaanem28S relative to a partial alignment of four anemones and two algal symbionts at A) 18S, and B) 28S rDNA genes. Intervening sequence between A) and B) not included. Sequence data for *H. magnifica* 1 was derived from GenBank (accession #AF050201).

Table 1. Moreton Bay sea anemone species used in the genetic analysis.

Collection Location	Latitude Longitude	Field Identification	Laboratory Identification	Genetic Source	Museum Reg. No.
Bird Island	27° 30′ S 153° 23′ E	*Entacmaea quadricolor* juv.	?*Anemonia* sp.	Whole animal	MTQ G58754
Flat Rock, N. Stradbroke I.	27° 24′ S 153° 33′ E	*Entacmaea quadricolor*	Not available	Tentacle	Whole spec. not coll.
Dunwich, flats in front of MBRS	27° 30′S 153° 24′E	*Stichodactyla haddoui*	Not available	Pedal disc & tentacle sample	Whole spec. not coll.
Shag Rock, N. Stradbroke I.	27° 24.85′S 153°31.59′E	*Heteractis malu*	*Heteractis malu*	Pedal disc & tentacle sample	MTQ G58749 QM Unreg.
Frenchmen's Beach	27° 25′ S 153° 32′ E	*Oulactis muscosa*	*Oulactis muscosa*	Pedal disc	MTQ G58756
Dunwich	27° 30′ S 153° 24′ E	*Macrodactyla doreensis*	*Macrodactyla doreensis*	Pedal disc & tentacle	MTQ G58748

collection of whole animals, which may not always be practical. Furthermore, histological analysis of sea anemones is time consuming and requires considerable expertise as some closely related species are almost impossible for the non specialist to identify, often resulting in incorrect taxonomic assignment (Stephenson 1928; Fautin 2000; Häussermann 2004).

Identification is further complicated by the fact that some species are virtually identical in appearance, distinguished by only one or two morphological features. For example, the two species *Heteractis malu* and *Heteractis crispa* are differentiated in the field on the basis of 1) column texture, which is firmer (leathery) in *H. crispa* than in *H. malu,* and 2) tentacle length, which is meant to be twice as long in *H. crispa* than *H. malu* (Fautin & Allen 1997). Both these characteristics can be misleading since the former is open to subjective interpretation if both species are not present side by side in the wild, while the latter may not necessarily be useful as the tentacles can be contracted at the time of collection/observation.

Alternatively, delineation of some species may be quickly achieved using appropriate molecular genetic methods (eg the Barcoding of Life initiative Hebert *et al.* 2003). However, previous genetic studies including sea anemone taxa have either only focused on questions pertaining to higher order anthozoan relationships (Won *et al.* 2001, Daly *et al.* 2003) or intraspecific population structure (Hunt & Ayre 1989). Numerous mitochondrial DNA genes such as COI (Fautin & Smith 1997), COIII and 16S rDNA (Geller & Walton 2001) have been used to infer phylogenetic relationships among the Actiniaria. However, mitochondrial gene sequence divergences within and among anthozoan families, including sea anemones, has been found to be significantly lower than other marine invertebrate species (Shearer *et al.* 2002). Barcoding studies also discovered that mitochondrial DNA evolved too slowly in sea anemones and other cnidarians for mtDNA differences to be an informative indicator of species (Hebert *et al.* 2003). Interestingly, Shearer *et al.* (2002) also found that, unlike all other metazoan taxa, substitution rates in anthozoan nuclear genes are much higher than in mitochondrial genes and therefore may be of greater utility in terms of species identification. Indeed, a number of other studies have suggested that the nuclear ribosomal (rDNA) gene complex incorporating 18S, ITS1, 5.8S, ITS2 and 28S could be ideally suited to examining below genus level relationships within the Actiniidae (McCommas 1991; Odorico & Miller 1997). Most recently Acuña *et al.* (2007) used the ITS region of rDNA in addition to morphology to distinguish between three species within the genus *Aulactinia*.

Molecular studies of sea anemones can be potentially complicated by the presence of symbiotic algae or zooxanthellae in the anemone tissue (Shearer *et al.* 2005) and possibly tissue

consistency (Pinto *et al.* 2000). If species possess zooxanthellae they are generally found in the gastrodermal tissues (i.e. tentacles and oral discs), although in some species they can be distributed heterogeneously throughout their hosts, being rare in only the pedal disc region or mesenteric tissue layers (Fautin & Smith 1997; Häussermann 2004). Therefore DNA extractions can contain both the host and algal genomes, which may cause confounding results especially for sequence data generated using broadly conserved or 'universal' primers (see Shearer *et al.* 2005). A study by Pinto *et al.* (2000) found tissue consistency to impinge on the success of extraction of DNA from sea anemones, due to hardness of tissue from being preserved in ethanol. They concluded that a slow and gradual digestion method was optimal for extraction.

Here we conduct a preliminary study to examine the utility of the rDNA gene complex in the identification of sea anemone species and test whether a known universal primer pair is sufficient for such studies or whether anemone specific primers will be required. Furthermore we use modern DNA extraction kits to see if previous problems associated with sea anemone DNA extraction can be circumvented.

MATERIALS AND METHODS
SPECIMEN AND TISSUE COLLECTION

Collection techniques included; removing anemones from rocks by chisel and hammer, scraping animals off rocks by fingernail or taking a small tissue sample from the animal in the wild for genetic analysis if identification was 100% positive in the field. Tissues for analysis were collected from twelve species (based solely on field identifications). Of these, six samples representing an initial five species were used in the genetic analysis (Table 1). Additional samples of *Heteractis malu* were collected from Shag Rock subsequent to the workshop.

In order to examine and minimise possible zooxanthellae contamination, small tissue samples of less than 5mm in length were excised from either the lower column/pedal disc or, where possible, separate tissue samples from both the tentacles and pedal disc region of each species were taken. All samples for genetic analysis were stored in 100% ethanol. Where whole specimens were collected, tissue samples were taken after animals were relaxed in magnesium chloride and before being preserved in 10% formalin: seawater. All ethanol preserved tissue samples were stored at -20°C until genetic analyses were performed. *Heteractis malu* specimens collected subsequent to the workshop were stored in 100% ethanol and kept at room temperature (approximately 21°C) only.

DNA EXTRACTION, PCR AND SEQUENCING

To test to the usefulness of modern DNA extraction kits with ethanol preserved sea anemone tissues, total genomic DNA was extracted from both tentacles and pedal disc tissues using DNeasy Tissue Kits (QIAGEN) as opposed to the far more labour intensive protocol of Pinto *et al.* (2000). Partial 18S rDNA, complete ITS1, 5.8S, ITS2 and partial 28S rDNA sequences were initially amplified using the primer pairs RA2 and ITS2.2 described by Wörheide (1998) RA2 is located in the flanking 3' end of the small subunit ribosomal gene (18S) and ITS2.2 in the 5' end of the large subunit ribosomal gene (28S). PCR amplifications were performed in 25 μl reaction volumes and contained to a final concentration: 1x Taq polymerase buffer, 2.5 mM MgCl$_2$, 0.2 μM each primer, 0.8 mM dNTPs and 0.75U of Taq polymerase. The use of the hot start polymerase HotMaster Taq (Eppendorf) required an initial denaturation at 94°C for 2 min prior to the commencement of the remaining cycle parameters; then followed 35 cycles of 94°C for 20 sec, 55–58°C for 20 sec, 65°C for 45 sec and a final extension 65°C for 5 min.

PCR products were gel purified using 'Perfect Prep' gel cleanup kit (Eppendorf) and forward and reverse sequencing reactions were carried out according to standard ABI PRISM dye-deoxy terminator sequencing protocols using Big Dye Terminator versions 1.1 and 3.1. Chromatographs were checked and all sequences were aligned using Se-Al v2.0a10 (Rambaut 1996). Estimates of sequence divergence including insertions (uncorrected p-distances) were calculated using the pairwise base distance function in PAUP* v4.0b10 (Swofford 2002). We verified the origin of the amplified sequence data by conducting a BLAST search in GenBank thus determining the phylogenetic affinity with sequences from other actiniarian or anthozoan species. Sequences

for this same region were also obtained from GenBank from two individuals of the species *Heteractis magnifica* (Accession no: AF050201 (*H. magnifica* 1) and AF050211 (*H. magnifica* 2)).

SEA ANEMONE PRIMERS

Based on the sequence results obtained from four of the six study species using the above described 'universal' primers and one of the *H. magnifica* sequences plus contaminating zooxanthellae sequences from the remaining two species (*Heteractis malu* and *Macrodactyla doreensis* — see Results), we designed two new primers. These primers were designed to be specific to sea anemones and located in regions of identical sequence among the sea anemone species (for which we had data) but mismatched the zooxanthellae sequences at 45-50% of sites (see FIG. 1). These two new primers *seaanem18S*: 5′ TTA GTG AGG ACT CCT GAT TGG C 3′ and *seaanem28S*: 5′ AGT CTC GCC TGA TCT GAG G 3′ lie within 50bp downstream from RA2 and ITS2.2 respectively. We tested the primers against the same six species used with the 'universal' primers. Amplification conditions, clean up and sequencing reactions with the new primers are identical to those described earlier.

RESULTS

DNA EXTRACTION

In contrast to Pinto *et al.* (2000) no problems were experienced extracting DNA from ethanol preserved sea anemone tissues using the DNeasy tissue kit. Prior treatment of the samples to remove ethanol was not required; nor did the tissues need to be homogenised in liquid nitrogen prior to the extraction process. Furthermore, total tissue digestion was completed within 1–3 hours at 55°C as recommended by the manufacture's protocol as opposed to the 72 hour period at 37ºC used by Pinto *et al.* (2000).

UNIVERSAL PRIMERS

An 800bp (approximately) PCR fragment was successfully amplified from all six sea anemone species and all tissue types using the universal primers RA2 and ITS2.2. Readable sequence data of the fragment (including the 3′ end of the 18S gene, full length ITS1, 5.8S gene and ITS2 and the 5′ end of 28S gene) was obtained from only three of the six species (?*Anemonia* sp, *M. doreensis* and *S. haddoni*). Partial/non-overlapping

sequences were obtained from the remaining three species (*E. quadricolor*, *H. malu* and *O. muscosa*). Not all tissue types generated readable sequence data. For example, sequences obtained from the pedal disc tissues of *H. malu* and *M. doreensis* were unreadable with evidence of multiple sequences present in the chromatograph (Table 2). This result was unexpected given that the amplified PCR product revealed a clear single band. However, readable sequence data was obtained from the tentacles of those same two species. BLAST searches of all readable sequences (either complete or partial) revealed strong matches (90-97% identity) with other sea anemone and/or anthozoan species in GenBank for only four of the six study species (Table 2). The sequence data obtained from the tentacles from *H. malu* and *M. doreensis* however, matched with almost 99% identity to other symbiotic algae sequences (e.g. *Symbiodinium* sp.) indicating preferential amplification of the zooxanthellae DNA in each of these species. Interestingly, the sequence data obtained from both the pedal disc and tentacles of *S. haddoni* were identical and BLAST searches of these and that obtained from the tentacles of *E. quadricolor* revealed closest similarity to other anthozoan species indicating that the host DNA had preferentially amplified and/or that zooxanthellae are either not present or in high enough density to mask the host DNA in both these species.

SEA ANEMONE PRIMERS

Amplification success using our primers *seaanem18S* and *seaanem28S* varied from that seen with the universal primers. Approximately 750 bp were obtained from five of the six anemone species; no PCR product amplified from *H. malu* regardless of tissue source (Table 2). For the three species for which either tentacle and/or pedal disc tissues were available, amplification success varied from species to species. No PCR product was obtained from *M. doreensis* tentacle DNA; in contrast, product amplified from the tentacle DNA of *E. quadricolor* and both tissue types for *S. haddoni* (Table 2).

The lack of amplification success for *H. malu* was surprising given that sequence data from the congeneric species, *H. magnifica*, was used in the alignment from which the new primers were designed and that the regions of both the

Table 2. PCR and sequence results obtained from anemone tissues using both the 'universal' primers and sea anemone specific rDNA ITS primers. Presence (+) or absence (–) of product is indicated.

Species	Tissue used in extractions	Preferential amplification and sequence obtained using 'Universal' primers		Preferential amplification and sequence obtained using sea anemone specific primers	
		Anemone DNA	Zooxanthellae DNA	Anemone DNA	Zooxanthellae DNA
?*Anemonia* sp.	Column / Pedal disc	+	–	+	–
Entacmaea quadricolor	Tentacle	+	–	+	–
Heteractis malu	Pedal disc	+	+	–	–
	Tentacle	–	+	–	–
Macrodactyla doreensis	Pedal disc	+	+	+	–
	Tentacle	–	+	–	–
Oulactis muscosa	Column / Pedal disc	+	–	+	–
Stichodactyla haddoni	Pedal disc	+	–	+	–
	Tentacle	+	–	+	–

18S and 28S genes where these primers are located are identical among all the actiniarian genera (bar one site in *O. muscosa*), for which sequence data was available. In order to see if we could amplify a product for *H. malu* but avoid zooxanthellae DNA contamination, we tried the sea anemone primers in combination with the previously successful universal primers; using *seaanem 18S* paired with ITS2.2 and *seaanem28S* paired with RA2. Successful amplification from *H. malu* DNA from both pedal disc and tentacles was only obtained using *RA2/seaanem28S*.

Sequences, either partial or complete, obtained from ?*Anemonia* sp., *O. muscosa* and *S. haddoni* using the new sea anemone primers were identical to those obtained using the universal primers, which had previously been confirmed as originating from host anemone DNA rather than their algal symbionts. BLAST searches of complete sequences from *M. doreensis* and *H. malu* obtained using anemone specific primers indicated greatest similarity to other anemones. Hence the anemone specific primers had been successful in circumventing the problems of zooxanthellae contamination. Curiously, *E. quadricolor* did not return readable sequence data suggesting that further optimisation of the sequencing reaction for this species and these primers may be required. For

H. malu, sequence obtained with RA2 revealed no mismatches in the 3' region of the 18S rRNA gene where *seaanem18S* is located that would explain why this primer did not work on this species. Further experiments may be required to secure successful amplification with both anemone specific primers on this species.

In summary, complete or overlapping sequences of the 18S–28S fragment were obtained from only 3 species (?*Anemonia sp.* (724 bp), *H. malu* (670 bp) and *S. haddoni* (734 bp)). Although partial or non-overlapping sequences were obtained from *E. quadricolor* (480bp from 18S), *M. doreensis* (523 bp: 300bp from 18S and 223bp from 28S) and *O. muscosa* (556bp: 285bp from 18s and 271bp from 28S), they were excluded from subsequent analysis due to incompleteness.

SPECIES IDENTIFICATION

Among the three species for which full sequences were obtained (including the two *H. magnifica* sequences obtained from GenBank) estimates of sequence divergence ranged from 0.14% within *H. magnifica* up to 25.10% between *H. magnifica* 1 and ?*Anemonia sp.* (Table 3). The average level of sequence divergence among species was 23.84% indicating that this region may indeed prove to be useful for species identification in sea anemones. The exception

was the comparison between *H. magnifica* and *S. haddoni*, where the divergence averaged only 1.7% (Table 3). This result was somewhat unanticipated given that it is significantly lower than the level of divergence found among the congeneric *H. magnifica* and *H. malu* sequences (ave 23.92%) and is therefore suggestive of possible taxonomic misidentifications. Considering that *H. magnifica* or *S. haddoni* cannot be taxonomically verified for this study due to specimen/tissue unavailability, it highlights the importance of using genetics in conjunction with traditional taxonomic methods.

The potential utility of this region for species identification is also evident from the example of ?*Anemonia* sp., which was tentatively identified in the field as resembling a juvenile *Entacmaea quadricolor* collected from Bird Island (Table 1). While only partial sequences were obtained from the adult *E. quadricolor* collected off Stradbroke Island, comparison of the sequences between the two specimens clearly showed they were significantly different (approx. 18% sequence divergence over 480bp) and possibly therefore two different species. Later histological analysis revealed that the the Bird Island specimen was not *E. quadricolor* as originally identified but may be ?*Anemonia* sp., although the exact identity of this species still awaits final taxonomic confirmation.

DISCUSSION

The ribosomal DNA gene complex has proved highly successful for species identification across an incredibly broad range of taxonomic groups including plants (Chase *et al.* 2005), fungi (Ristaino *et al.* 1998; Iwen *et al.* 2002), digenean parasites (Nolan & Cribb 2005) and mosquitos (Collins & Paskewitz 1996). It has even been used recently to identify commercial crustacean species from larvae collected in plankton surveys (Wang *et al.* 2006). In this study we investigated for the first time, the utility of this region for identification of sea anemone species and the potential problems of using universal primers in species, which contain algal symbionts.

While of a preliminary nature, our results showed high levels of sequence divergence among species using this region compared with divergence estimates an order of magnitude lower within a species indicating that it may indeed be ideal for assisting with sea anemone species identification. The questions at what taxonomic level and how useful this region may be for resolving phylogenetic relationships among sea anemone species was not the focus of this study but should certainly be investigated as more sequences become available. Acuña *et al.* (2007) used phylogenetic tools rather than estimates of sequence divergence to distinguish between different *Aulactinia* species and found extremely short branch lengths among individuals within a species compared to those between species.

The usefulness of conserved `universal' primers clearly depends on the species and tissue type available for analysis. However, as shown by the results obtained from *H. malu* and *M. doreensis*, extraction of `uncontaminated' host DNA from samples taken only from pedal disc tissues clearly should never be assumed. In order to guarantee that host DNA is amplified alone, use of primers specific to sea anemones are recommended; if not on their own then at least in combination with another universal primer. The extent to which the primers designed

Table 3. Estimates of sequence divergence among species for which the complete 18S–28S fragment was obtained (max 758bp). Sequences for *H. magnifica* obtained from GenBank. *Specimen collected subsequent to Workshop.

	?*Anemonia* sp.	*H. magnifica* 1	*H magnifica* 2	*H. malu*	*S. haddoni*
?*Anemonia* sp.	–				
H. magnifica 1	25.10%	–			
H. magnifica 2	24.93%	0.14%	–		
*H. malu**	21.60%	23.84%	23.99%	–	
S. haddoni	24.42%	1.64%	1.77%	22.98%	–

for this study will work across all actiniarians remains to be seen. Further preliminary PCR testing using *seaanem18S* and *seaanem28S* on another seven species from Moreton Bay, and representing another seven actiniarian genera, proved highly successful with strong amplicons produced in all seven species. Only subsequent sequencing will confirm whether or not the host DNA has been successfully targeted.

Modern DNA extraction kits also seem highly useful for overcoming any difficulties associated with DNA extraction from ethanol preserved sea anemone tissues. Why we experienced so few problems compared with the earlier work of Pinto *et al.* (2000) is unclear. It may be that we were able to work with tissues from recently ethanol preserved specimens, rather than ones, that had been in ethanol for an extended time.

Finally, a number of aspects of this study reinforce the value of being able to combine histological analysis with genetic testing to irrefutably verify a species' identity, especially given the embryonic stage of developing genetic markers for this group. In the case of a supposed juvenile *E. quadricolor*, the genetic data strongly indicated an incorrect field identification, and a subsequent histological analysis proved this to be so, identifying it instead as a probable *Anemonia* species. Furthermore, the curious result showing much greater sequence divergence between the two *Heteractis* species than that detected between *Heteractis magnifica* and *Stichodactyla haddoni* cannot, frustratingly, be resolved further. While again indicative of possible misidentifications, the *H. magnifica* sequences available on GenBank are not associated with registered specimens and the *S. haddoni* cannot be analysed histologically as the whole animal was not collected from the field.

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Ancient chemosynthetic bivalves: systematics of Solemyidae from eastern and southern Australia (Mollusca: Bivalvia)

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ABSTRACT

The systematics of the chemosymbiotic bivalve mollusc family Solemyidae in Australia are reviewed using morphological characters and some molecular data. Recognised world genera/subgenera are redefined on the basis of ligament characters and features of the posterior aperture and an additional new subgenus *Solemya (Austrosolemya)* (type species *S. australis*) is proposed. Four species are recognised from eastern Australia, including three from Moreton Bay: *S. (Solemyarina) terraereginae, S (S.) velesiana*, and *Solemya moretonensis* sp. nov., with another undescribed species represented by a single specimen from Moreton Bay. The large *Solemya (Austrosolemya) australis* is distributed around southern and southwestern Australia while two further species, from South and Western Australia, are recognised on the basis of molecular data and to some extent morphology, but not formally named. For the first time, major features of the anatomy, including details of ctenidia and bacteriocytes, of an Australian solemyid (*S. (Solemyarina) velesiana*) are described. ❑ *taxonomy, revision, new species, Solemya Moreton Bay, chemosynthesis*

The Solemyidae is one of five bivalve families known to possess endosymbioses with sulphide-oxidising, chemoautotrophic bacteria housed in the gills (Fisher 1990; Distel 1998; Stewart & Cavanaugh 2006). Morphologically, Solemyidae are highly distinctive and unusual bivalves, with an elongate, near cylindrical shape and covered with glossy, thick, brown periostracum extended as a broad, pleated, flexible fringe. They have thin, lightly calcified, organic-rich, flexible, edentulous shells, with extensive ventral mantle fusion forming a large anterior aperture, through which protrudes the large, papillae-fringed foot, and a small posterior aperture. Large ctenidia occupy most of posterior mantle cavity and the gut is much reduced, or absent in some species. Solemyids are also capable of swimming by jet propulsion by expulsion of water through the posterior aperture (Reid 1980).

All species investigated in any detail possess endosymbionts (Kreuger & Cavanaugh 1997). Likely vertical transmission of symbionts through eggs is known for *Solemya velum* (Kreuger *et al.* 1996). The biology of the chemosymbiosis of solemyids has been much studied with the north American *Solemya velum* Say, 1822 and the gutless species, *Solemya reidi* Bernard, 1980, attracting most attention (Reid 1980; Powell & Somero 1985; Fisher & Childress 1986; Gustafson & Reid 1986; Conway *et al.* 1989; Stewart & Cavanaugh 2006). While a number of solemyids characteristically have small or reduced

alimentary systems (Stempell 1899; Owen 1961; Kuznetsov *et al.* 1990; Reid 1998), the gutless condition is known in *Acharax alinae* Métivier & Cosel, 1993, *Petrasma atacama* Kuznetzov & Schileyko, 1984, *Acharax eremita* Kuznetsov & Schileyko, 1984, and *Petrasma borealis* (Totten, 1834) (see Kuznetzov & Schileyko 1984; Conway *et al.* 1992; Métivier & Cosel 1993).

There are around 30 described species in the family, although it is certain that there are undescribed species from deepwater cold seeps (see Neulinger *et al.* 2006) as well as unregarded small species in tropical shallow waters. Most shallow water solemyids are small, with lengths of less than 30 mm, but *Acharax* species from deeper water attain larger sizes — *Acharax bartschii* Dall, 1908 reaches 210 mm shell length, *Acharax alinae* 135 mm (Métivier & Cosel 1993) while a fossil *Acharax* from the Miocene measured a massive 300 mm (Kanie & Kuramochi 1995).

Solemyids are geographically widespread from the tropics to temperate latitudes and with a depth range from the intertidal to 5350 m (Fujiwara 2003). They inhabit muds, silts and sands (Stanley 1970; Conway *et al.* 1992; Krueger *et al.* 1996) but are often associated with organically enriched habitats such as seagrass beds (Stanley 1970; Reid & Brand 1987), wood pulp accumulations (Reid 1980), human hair in sewage dumps (Coan *et al.* 2000), and deep-sea cold seeps and vents (Métivier & Cosel 1993; Neulinger *et al.* 2006).

Solemyidae are probably geologically the oldest of the chemosymbiotic bivalves with a fossil record extending back into the Lower Palaeozoic. The earliest known is *Ovatoconcha* from the early Ordovician (Arenig ca 475 mya) (Cope 1996a), while other solemyids are known from the middle Ordovician and younger rocks (Pojeta 1988). The general similarity in morphology of these fossils to living species suggests that they possessed similar life habits.

In view of their life habits and antiquity, the relationships of solemyids to other bivalves are of considerable interest. Most classifications place the Solemyidae along with the Manzanellidae (=Nucinellidae) in the superfamily Solemyoidea, and together with the Nuculoidea and Nuculanoidea in the subclass Protobranchia, occupying a basal position relative to all other bivalves (Yonge 1939; Pojeta 1988; Starobogatov 1992; Morton 1996; Cope 2000; Zardus 2002). Alternatively, some classifications suggest placement of Solemyoidea in a separate subclass (Cox 1969; Cope 1996b; Amler 1999). Cladistic analyses of morphological characters have grouped Solemyidae and Nuculidae as sister taxa within the subclass Protobranchia (Salvini-Plawen & Steiner 1996; Waller 1998; Giribet & Wheeler 2002). Molecular evidence indicates that either Solemyidae form a monophyletic group (weakly supported) with Nuculidae and Nuculanoidea (Steiner & Hammer 2000) or, alternatively, Solemyidae and Nuculidae group as sister taxa but are distinct from Nuculanoidea and the rest of the bivalves (Giribet & Distel 2004, fig. 3.6). In this latter analysis, the clade Solemyidae + Nuculidae groups with other conchiferan classes Gastropoda, Scaphopoda and Cephalopoda rather than with the rest of the bivalves that form a monophyletic clade.

Despite the biological interest of solemyids, their systematics is confused with species appearing very similar to each other on external characters. Internally, there are differences in the morphology of the hinge and ligament, such that ligamental characters have been used as a basis for subgeneric and generic separation but interpretations have differed (Dall 1908a,b; Cox 1969; Bernard 1980; Lamprell & Healy 1998). There has been no attempt to incorporate anatomical characters into systematics although some prominent features such as the posterior pallial apertures are potentially character-rich. Molecular data are desirable for future systematic studies of Solemyidae but, as yet, few species have been analysed (Giribet & Distel 2004; Neulinger *et al.* 2006).

AUSTRALIAN SPECIES

Three species of Solemyidae have been described from Australia: *Solemya australis* Lamarck, 1818, from south western Australia; *S. terraereginae* Iredale, 1929, from Queensland and *S. velesiana* Iredale, 1931, from New South Wales. Inexplicably, Lamprell & Healy (1998) synonymised the tropical *S. terraereginae* with *S. australis* from southern Australia, with this decision followed in other publications, e.g. the Database of Indo-Pacific Marine Molluscs <http://data.acnatsci.org/obis/search.php>. They

also placed *Solemya australis* and *S. velesiana* into separate subgenera *Solemya* s.s. and *Solemyarina*.

Symbiotic bacteria were first recorded in the gills of *Solemya velesiana* and *S. australis* by Reid & Brand (1987) who also provide some anatomical information for the two species. Their samples of *S. velesiana* came from Orpheus I., Queensland and they may have confused the species with *S. terraereginae*. Both small and large solemyids from southern and western Australia were referred to *S. australis* but it seems likely that at least two species have been confounded. Later, Kreuger & Cavanaugh (1997) sequenced the bacterial symbionts of *S. terraereginae* from Lizard Island and gave TEM details of their location in the gill filaments.

From samples collected during the Marine Biological Workshop in Moreton Bay, we recognised three small *Solemya* species; one was regularly encountered in sediment from intertidal seagrass habitats; another smaller species was recovered from slightly deeper water grab samples outside the Bay and a third was represented by only a single specimen, again from a grab sample, but within the Bay. In attempting to identify these bivalves and samples from two other sites in South and Western Australia it became apparent that the systematics of Solemyidae from Australia needed some updating for the original descriptions and illustrations of the described species were poor.

In this paper we review the systematics of Australian Solemyidae, provide new illustrations of the relevant type material, identify the Moreton Bay species and discuss the status of other small solemyids from Australia. We also review the characters of living solemyid genera providing new illustrations of ligament and apertural characters. We present new molecular sequences of 18S and 28S rRNA and cytochrome B genes for the most abundant of the Moreton Bay species and compare them with sequences from other putative species collected in South and Western Australia and with published sequences from other *Solemya* from North America and *Acharax* spp. from deeper water. Additionally, we provide details of the anatomy of *Solemya velesiana* from Moreton Bay and compare it with other *Solemya* species from Australia and elsewhere.

MATERIAL AND METHODS

COLLECTION OF SAMPLES AND HABITATS

Queensland Moreton Bay. *Solemya (Solemyarina) velesiana* was sieved from intertidal seagrass-covered sand between Dunwich and Amity Point, North Stradbroke Island, Moreton Bay in February 2005. A single specimen of another unnamed species was dredged from mud at Banana Bank in southern Moreton Bay. *Solemya moretonensis sp. nov.* was obtained from grab samples seaward of Moreton Island.

Queensland, Lizard Island. *S. (Solemyarina) terraereginae* was sieved from intertidal lagoon sands with a sparse covering of the seagrass *Halophila* in November 2000.

South Australia. A sample of the small solemyid *S. (Solemyarina)* species A was collected intertidally from a narrow, silt covered, rock platform at Anchorage Bay, Victor Harbor, South Australia in February 2001.

Western Australia. Three small individuals of *S. (Solemyarina)* species B were sieved from mud covered in dead algae, in a mangrove-fringed channel, at Little Lagoon, Denham, Shark Bay in July 2004.

ANATOMY

General anatomy of specimens from Moreton Bay and Lizard Island was studied by serial thin sections of decalcified, formalin-fixed specimens. Sections were cut at 8 mm and stained with Masson's trichrome. For examination of the ligaments, hinge areas of the solemyids were dissected from the shell and imaged beneath ethanol with transmitted light. For scanning electron microscopy, animals were fixed in a 2.5% solution of glutaraldehyde in phosphate buffer or 5% formalin in seawater. The animals were dissected and the tissues sliced with a razor blade. Tissue pieces were then dehydrated through ascending concentrations of acetone, critical point dried, mounted on stubs, coated with gold and examined by SEM (Philips FE X30).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING.

Animals for molecular analysis were preserved in absolute ethanol. DNA was extracted and portions of two genes, the nuclear 18S rRNA and 28S rRNA genes, were amplified and sequenced following the methods of Williams

& Ozawa (2006). One sequence of the mito-chondrial cytochrome B (cytB) gene was obtained from each Australian *Solemya* sample using primers cytb-F (GRGGKGCTACKGTAATTACTAA) and cytb-R (AAATAYCAYTCNGGCTGRATATG), following the amplification conditions for COI in Williams & Ozawa (2006). Sequence reactions were performed directly on purified PCR products using a BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyser automated capillary sequencer. Sequences were verified by forward and reverse comparisons.

Sequences were edited and aligned following methods in our previous studies (Williams *et al*. 2004; Taylor *et al*. 2005). Poorly aligned sites were identified using Gblocks (0.19b, Castresana 2000) and removed from analyses. After removal of ambiguous blocks of data, a total of 920 bp of sequence from 18S rRNA remained to be used in phylogenetic analyses of the large taxon set (90% of 1013 bp in the original alignment) and 1469 bp of 28S rRNA (99% of 1477 bp in the original alignment). The alignment of cytB was unambiguous. Pairwise distances were calculated among the three cytB sequences using Kimura's 2-parameter (Kimura 1980) distance.

Phylogenies were constructed for the nuclear genes using maximum likelihood (ML) as implemented in PAUP* (Swofford 2002). The models used were K80+ G (t ratio = 2.0331, α = 0.1928) for 18S rRNA and GTR+G (Base sequences = (0.2324, 0.2543, 0.3124) Nst = 6 Rmat=(0.8306, 1.4938, 0.9609, 0.5928, 5.5177) α = 0.2479) for 28S rRNA, which were among several options suggested by MrModelTest (v 2.1, J. Nylander (http://www.abc.se/~nylander/). Taxa were added randomly with ten replicates and a heuristic search option used with nearest neighbour interchange (NNI) branch-swapping. On completion of this analysis, it was repeated using the tree obtained from the first search, and tree bisection-reconnection (TBR) branch-swapping. Nodal support was tested by bootstrapping with ML with ten random replicates of taxa, TBR branch-swapping and with neighbour-joining bootstrap (NJ) using ML distances, both with 1,000 replicates.

Voucher material of the sequenced species is lodged in the Natural History Museum, London, registration numbers 20060149–152.

ABBREVIATIONS

AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; MNHN, Museum National d'Histoire Naturelle, Paris; QM, Queensland Museum, Brisbane; WAM, Western Australian Museum Perth.

SYSTEMATICS

Identification and classification of solemyid species has proven especially troublesome because of the overall similarity of external shell features within the group, coupled with the delicate fragile shells, thick, brown periostracum and the lack of standard bivalve features such as shell sculpture and hinge teeth. Most 20th century authors used characters of the internal ligament in an attempt to define supraspecific groupings. Dall (1908a, b) was the first to recognise differences in ligament morphology amongst solemyids and proposed a subgeneric classification of *Solemya* species based largely on the structure of the ligament and supporting calcified structures. He defined *Solemya* s.s. as having internal lateral ligament extensions located anterior to the chondrophore and the subgenus *Petrasma* with the ligament not exposed internally anterior to the chondrophore, while *Acharax* has an external ligament. However, his concept of *Solemya sensu stricto* was based on *S. australis* rather than *S. togata* (Poli, 1795) as the type species and the two taxa are very different in ligament structure, the latter lacking the anterior lateral extensions as lobate or linear structures.

Later, Iredale introduced two more genera; *Solemyarina* Iredale, 1931 (type *S. velesiana*) and *Zesolemya* Iredale, 1939 (type *S. parkinsonii*), also based on the structure of the ligament, but his diagnoses were very brief. Cox (1969) unraveled much of the confusion and correctly illustrated the ligament of *S. togata* as the type species of *Solemya*. Unfortunately, the ligament of *S. australis* was illustrated as the type of *Solemyarina* rather than *S. velesiana*. Further confusion was added by Bernard (1980, figs 1–3) who classified *Solemya reidi* into *Solemya*, despite the anterior lateral extensions. Confusion has continued with Lamprell & Healy (1998) also placing *S. australis* in *Solemya s. s.*
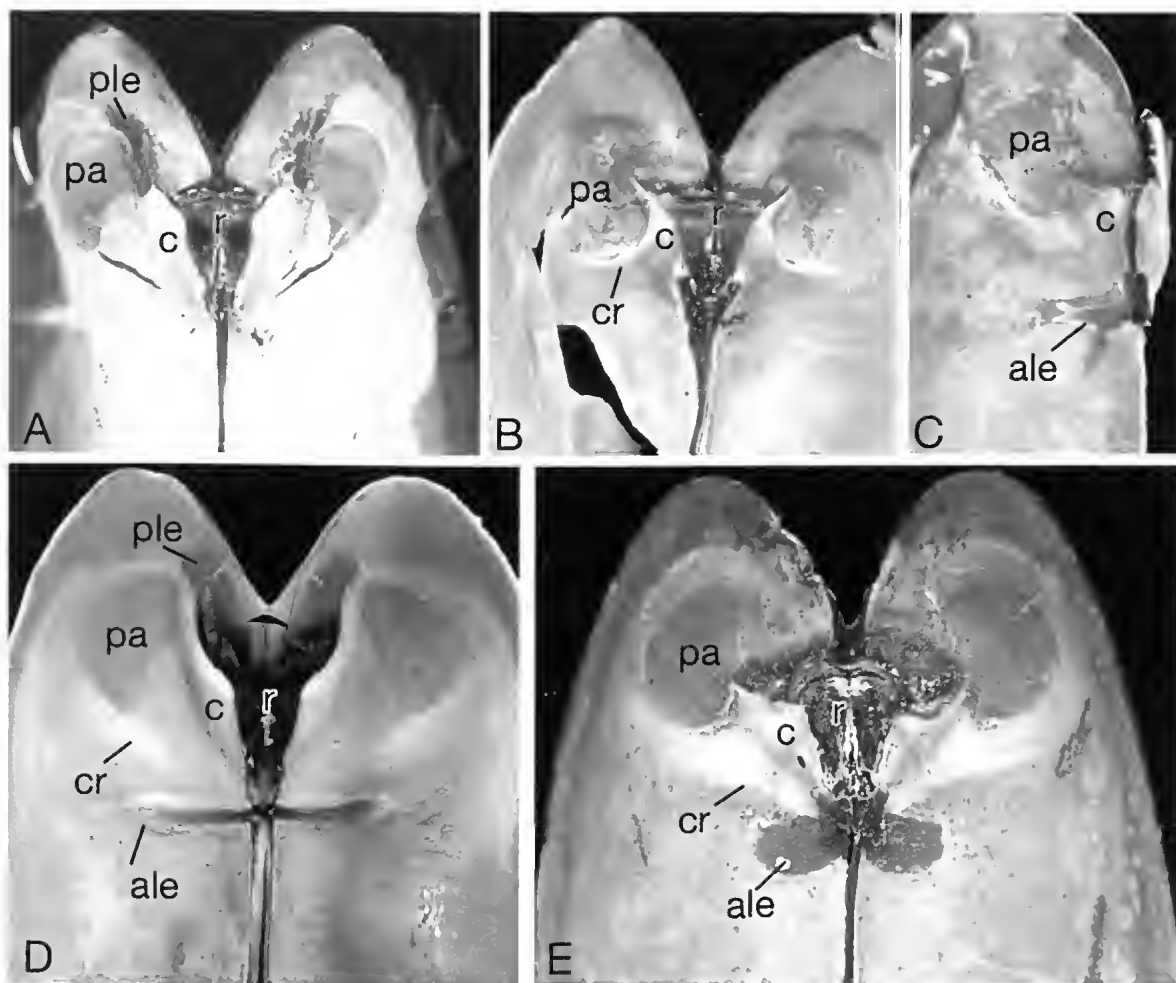
FIG. 1. Internal ligamental areas of type species of genera and subgenera of Solemyidae. **A**, *Solemya*: *Solemya togata*, Malta (BMNH-78.5.10.220); **B**, *Petrasma*: *S. (Petrasma) velum*, Narragansett, Rhode Island, USA (used as a proxy for *S. borealis* as no material suitable for imaging available); **C**, *Solemyarina*: *S. velesiana*, Port Jackson, Sydney (BMNH-95.3.7.17–19); **D**, *Zesolemya*: *S. parkinsonii* (syntype BMNH-1852.3.16.46–48), New Zealand; **E**, *Austrosolemya*: *Solemya australis* (often incorrectly illustrated as the type of *Solemya* s.s.), Australia, Cuming Collection (BMNH). ale = anterior lateral extension; c = chondrophore; cr = chondrophoral ridge; pa = posterior adductor scar; ple = posterior ligament extension; r = resilifer. Scale bars: A, D, E = 5 mm; B, C = 2 mm.

Below we list the currently accepted genera and subgenera of Solemyidae with a brief summary of their ligament characters. Figure 1 shows the main features of the ligament in these taxa. Additionally, our observations suggest that characters of the posterior aperture, such as numbers and arrangement of papillae may have some potential in solemyid systematics, as originally observed by Morse (1913) in *Solemya velum* and *S. borealis*. We also include brief descriptions and illustrations of these based on

type species of the genera. Following Stempell (1899), the apertural papillae can be described in two groups — the dorsal, suprasiphonal papillae are paired and located above or at the dorsal margin of the aperture, with in most species, a single papilla located dorso-centrally (Fig. 2A-G); siphonal papillae either totally surround the aperture or just fringe the ventral margin. The suprasiphonal papillae are often larger than the siphonal papillae with the ventral pair always longer.

For the present, and pending further analysis, we regard *Solemyarina*, *Petrasma*, *Zesolemya* and *Austrosolemya* as subgenera of *Solemya*.

Solemya Lamarck, 1818

Type species: *S. mediterranea* (Lamarck 1818) = *Tellina togata* Poli, 1795 (by subsequent designation Children, 1823)

Remarks. The chondrophore is large (Fig. 1A) with a broad, triangular resilium and supporting ribs around the posterior adductor are absent. Narrow strips of ligament are visible along both ventral edges of chondrophore and anterior lateral extensions of ligament are absent. Posteriorly, the outer ligament layer extends as two narrow tongues around the dorsal
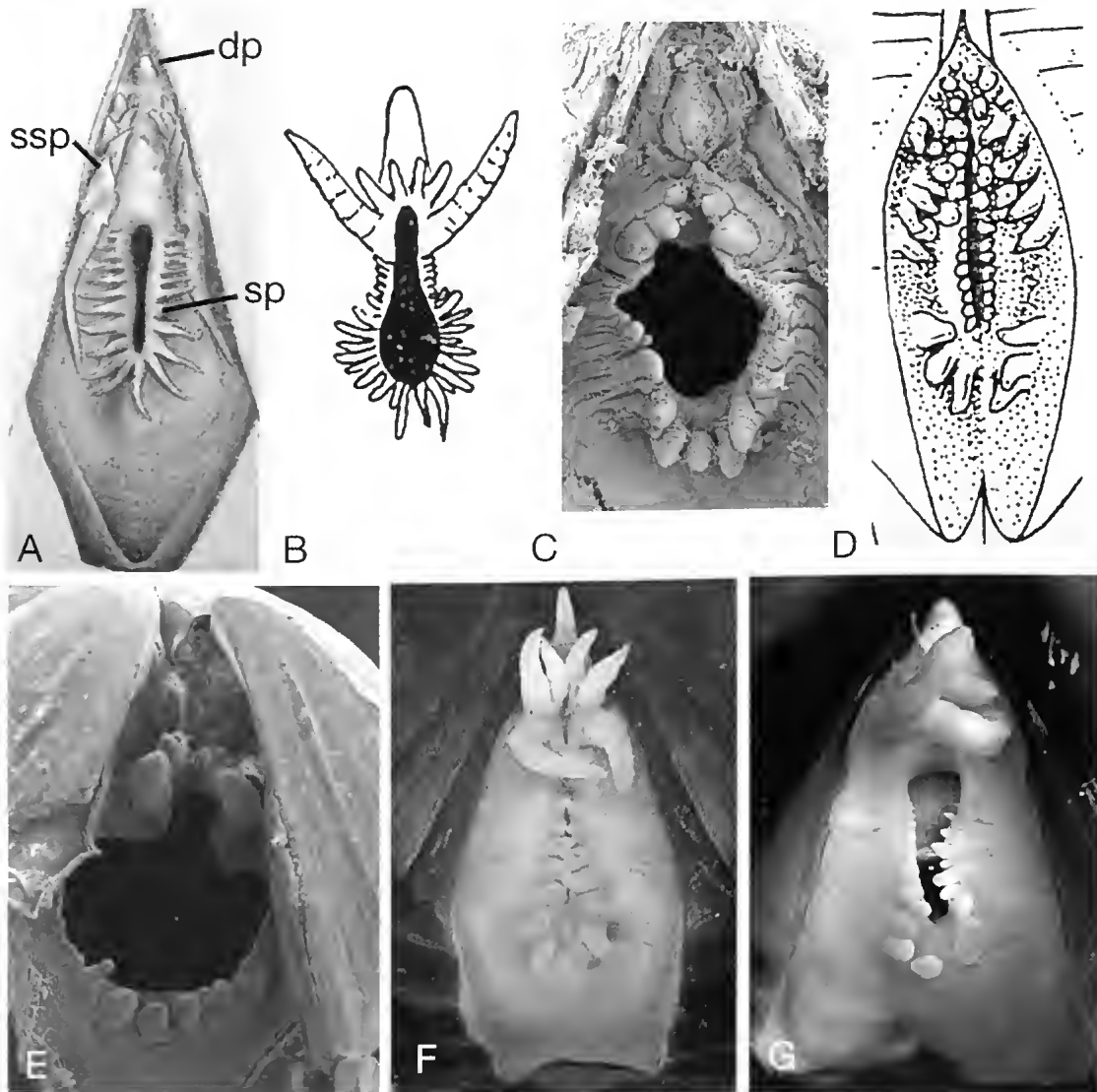
FIG. 2. Posterior apertures of Solemyidae: type species of subgenera. **A**, *Solemya: S. togata* (from Stempell, 1899, fig. 2); **B**, *Petrasma: Solemya borealis* (from Morse 1913, fig. 21; **C**, *Petrasma velum*, Cape Cod, USA (original); **D**, *Acharax*: proxy for type species *A. eremita* (from Kuznetsov & Schileyko, 1984 fig. 3b); **E**, *Solemyarina: S. velesiana*, Moreton Bay (original); **F**, *Zesolemya: Z. parkinsonii* (from Beedham & Owen, 1965, pl. 1, fig. 2); **G**, *Austrosolemya: A. australis*, Esperance (original). dp = dorsal papilla; ssp = suprasiphonal papillae; sp = siphonal papillae. Scale bars: A, F, G = 5 mm; C = 2 mm; E = 0.5 mm; B, D, none given in original publication.

edge of the adductor scars (Fig. 1A). Stempell's (1899 fig. 2) figure of the posterior aperture *S. togata* shows (Fig. 2A) a single unpaired posterior papilla, seven pairs of suprasiphonal papillae, with the most ventral of these very long and slender. The siphonal opening is fringed by 20–22 pointed, slender papillae that are slightly longer on the ventral margin.

Solemya (Solemyarina) Iredale, 1931

Type species: *Solemya velesiana* Iredale, 1931 (by original designation).

Remarks. The genus was originally proposed to separate smaller eastern Australian species – *S. terraereginae* and *S. velesiana* from *Solemya*. The dorsal margins of the chondrophore are almost parallel (Fig. 1C) with a narrow resilium. The posterior margin of the chondrophore is slightly sinuous and not extended posteriorly. A low, thin chondrophoral rib extends around the anterior margin of the posterior adductor scar. The ligament anterior to the chondrophore forms a broadened, heart-shaped area, with narrow, linear, lateral extensions (Fig. 1C). The posterior aperture of *S. velesiana* (Fig. 2E) has a single, short dorsal papilla, three to four pairs of short, suprasiphonal papillae, with the ventral pair slightly larger, and 9–10 short siphonal papillae around the ventral margin, with the most ventral of these slightly larger.

Solemya (Austrosolemya) subgen. nov.

Type species: *Solemya australis* Lamarck, 1818 (here designated).

Remarks. For details see below under Australian species.

Solemya (Petrasma) Dall, 1908

Type species: *Solemya borealis* Totten, 1834 (by original designation), northwestern Atlantic.

Remarks. The chondrophore (Fig. 1B) has posterior and anterior supporting ridges that form an arcuate cavity around antero-dorsal margin of the posterior adductor muscle. The resilium is broad and triangular. Anterior lateral extensions of ligament are absent (Fig. 1B). The only illustration of the posterior aperture of *S. borealis* available is a sketch by Morse (1913 fig. 21). This shows (Fig. 2B) three pairs of suprasiphonal papillae, with the ventral pair long; the aperture is fringed by

about 30 shorter siphonal papillae that are larger ventrally. *Solemya (Petrasama) velum*, often taken as a proxy for the type species, has similar ligament characters to *S. borealis* but the suprasiphonal papillae are shorter (Fig. 2C).

Solemya (Zesolemya) Iredale, 1939.

Type species: *Solemya parkinsonii* Smith, 1874 (by original designation), New Zealand. (Usually synonymised with *Solemyarina* (Cox, 1969) or *Solemya* (Bernard, 1980)

Remarks. Iredale distinguished *Zesolemya* from Australian *Solemyarina* species on basis of narrow posterior extensions of the ligament (Fig. 1 D ple) and the chondrophore bifurcating around the posterior adductor scar. Also, the dorsal extension of the chondrophore reaches the posterior margin of the adductor scar (Fig. 1D). Prominent anterior, lateral, linear extensions of the ligament are present (Fig. 1D ale). Based on Beedham & Owen's figure (1965, pl. 1, fig. 2) there are 3–4 pairs of long suprasiphonal papillae, the longest ventral, with around 20 large siphonal papillae that are longer ventrally (Fig. 2F).

Acharax Dall, 1908

Type species: *Solemya johnsoni* Dall, 1891 (by original designation). NE Pacific.

Remarks. The chondrophore (not figured but see Pojeta, 1988, plate 2, figs 2–5) is narrow and does not bifurcate but the shell is thickened around the posterior adductor scar. The ligament does not extend internally. The only illustration available of a posterior aperture is for *Acharax eremita* (Kuznetsov & Schileyko, 1984: fig. 3B) and this is far more complex than any *Solemya* species (Fig. 2D). There are three rows of paired suprasiphonal papillae; the inner margin of the aperture is fringed with short, siphonal papillae and six larger papillae lie ventral to the aperture.

THE AUSTRALIAN SPECIES

In this section we review the Australian species. Adult *S. (Austrosolemya) australis* can be easily recognised by their larger size, but smaller species are less readily distinguished by external shell characters. Thus, in the brief descriptions below, we focus on ligament structure and characters of the posterior aperture. Pending a
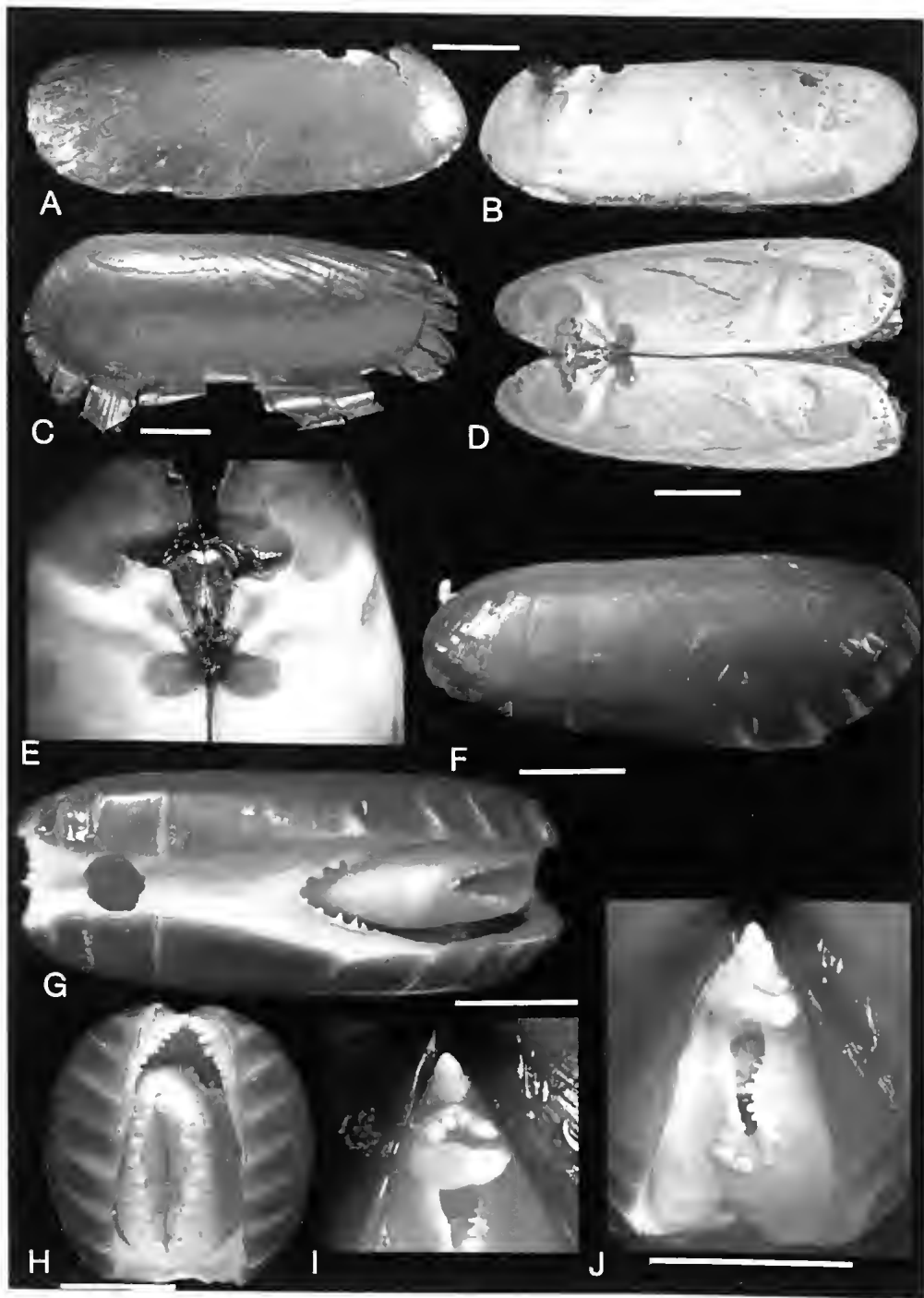
FIG. 3. *Solemya (Austrosolemya) australis* (Lamarck, 1818). **A–B**, syntype, King George Sound, Albany, Western Australia (MNHN). **C**, right side, Australia (MacAndrew Collection, BMNH); **D**, shell interior, Australia (Cuming Collection, BMNH); **E**, detail of internal ligamental area (BMNH); **F–J**, Dempster Head, Esperance, Western Australia (WAM -S16037); **F**, right lateral view; **G**, ventral view, circular hole in mantle is an artifact; **H**, anterior view showing papillae of dorsal pedal gape; **I**, dorsal and suprasiphonal papillae; **J**, posterior aperture with suprasiphonal and siphonal papillae. Scale bars = 10 mm.

global revision of the Solemyidae we classify the species within subgeneric divisions of *Solemya*.

Solemya (*Austrosolemya*) subgen. nov.

Type Species: *Solemya australis* Lamarck,1818

Diagnosis. Large *Solemya* with internal ligament possessing lobate anterior extensions, a broad triangular resilium and strong chondrophoral ridges. (Fig. 1E).

Remarks. Another included species might be *Solemya reidi* Bernard, 1980, that has a similar ligament structure (Bernard 1980, fig. 1; Coan *et al*. 2000, fig. on p. 64).

Etymology. From *australis* meaning southern

Solemya (*Austrosolemya*) *australis*
Lamarck, 1818
(Figs 3 A–J)

Solemya australis Lamarck, 1818: 489.
Solemya australis — Cotton & Godfrey, 1938: 28, fig. 4.
Solemya (Solemya) australis — Lamprell & Healy, 1998: 42, fig. 48.

Material Examined. SYNTYPE: left valve, length 51 mm, King George Sound, Albany, Western Australia (on label - Port Roi George) (MNHN). OTHER MATERIAL: Victoria: Portland (AMS C92892); South Australia: Adelaide (BMNH 88.2.29.207), Glenelg (AMS C92893); Largs (AMS C92891), Holdfast Bay (AMS C47078); Kangaroo I. (AMS C143993); Spencer Gulf (AMS); West Beach (AMS). Western Australia: Esperance (WAM); Albany, Middleton Beach (AMS C 71447); Fremantle (WAM); Rottnest I. (WAM).

Description. Shell large, to 60 mm, dorsal and ventral margins sub-parallel. Periostracum thick, chestnut brown, with conspicuous raised, brown rays. Darts within periostracal pleats, cream coloured. Internal ligament, relatively short, dorsal edges of chondrophore diverging posteriorly to accommodate thick pad of inner ligament, posterior edge of chondrophore sinuate; chondrophoral buttress prominent around anterior margin of adductor muscle; anterior of ligament with subcircular lateral extensions (Figs 1E; 3E). Posterior aperture (Figs 3I, J) with a large, dorsal papilla, three pairs of suprasiphonal papillae, the ventral pair much longer and thicker, and up to 20 siphonal papillae that are larger around the ventral margin.

Distribution. Southern Australia — Victoria to Fremantle and Rottnest Island

Remarks. We are uncertain of the relationship of this species to the east coast *Solemyarina*. *S. (A.) australis* is much larger than any of the east coast species and the ligament differs in having a broadly triangular resilium, prominent, lobate, anterior lateral ligament extensions (Figs 1E, 3E) and a massive projection of the chondrophore forming a ridge round the anterior margin of the adductor muscle. The posterior aperture has larger and more numerous papillae (Figs 2G, 3 I, J).

Solemya (*Solemyarina*) *velesiana*
Iredale, 1931
(Figs 4A–H)

Solemya velesiana Iredale, 1931: 201. (not figured).
Solemyarina velesiana — Iredale, 1931: 202.

Material Examined. HOLOTYPE: East side of the Spit, Middle Harbour, Sydney New South Wales (AMS C7476). Length 9.5 mm. Described from Sydney area, without specific locality, but Sydney Harbour written on label — not Green I. as cited in Reid & Brand (1987: 42). OTHER MATERIAL: Queensland. North Stradbroke I., Moreton Bay (BMNH); New South Wales. Sydney Harbour (BMNH 95.3.7.17-19); Green I., Jervis Bay (AMS); Broulee (AMS); Twofold Bay (AMS). Victoria. Portsea, Port Philip Bay (AMS); South Australia. (cf *velesiana*) Kangaroo I. (AMS).

Description. Small, length to 16 mm, elongate, slightly broader anteriorly, periostracum pale brown with around six anterior and posterior white rays, corresponding to raised ridges on shell, visible through periostracum. Internal ligament with dorsal edges of chondrophore parallel and narrowly separated; a low chondrophoral ridge wraps around anterior margin of adductor muscle scar; short, linear, anterior lateral extensions of ligament present. Posterior aperture has three to four pairs of short, suprasiphonal papillae, the ventral pair slightly larger. There are about nine small, siphonal papillae around the ventral margin of the aperture. A single unpaired papilla lies dorsal to the aperture.

Distribution. Moreton Bay, Queensland to South Australia.

Habitat. In Moreton Bay, *S. (S.) velesiana* was shallow burrowing in seagrass (*Cymodocea, Zostera, Halodule* and *Halophila*) covered sands where it co-occurred with other chemo-symbiotic bivalves, the lucinids, *Pillucina*
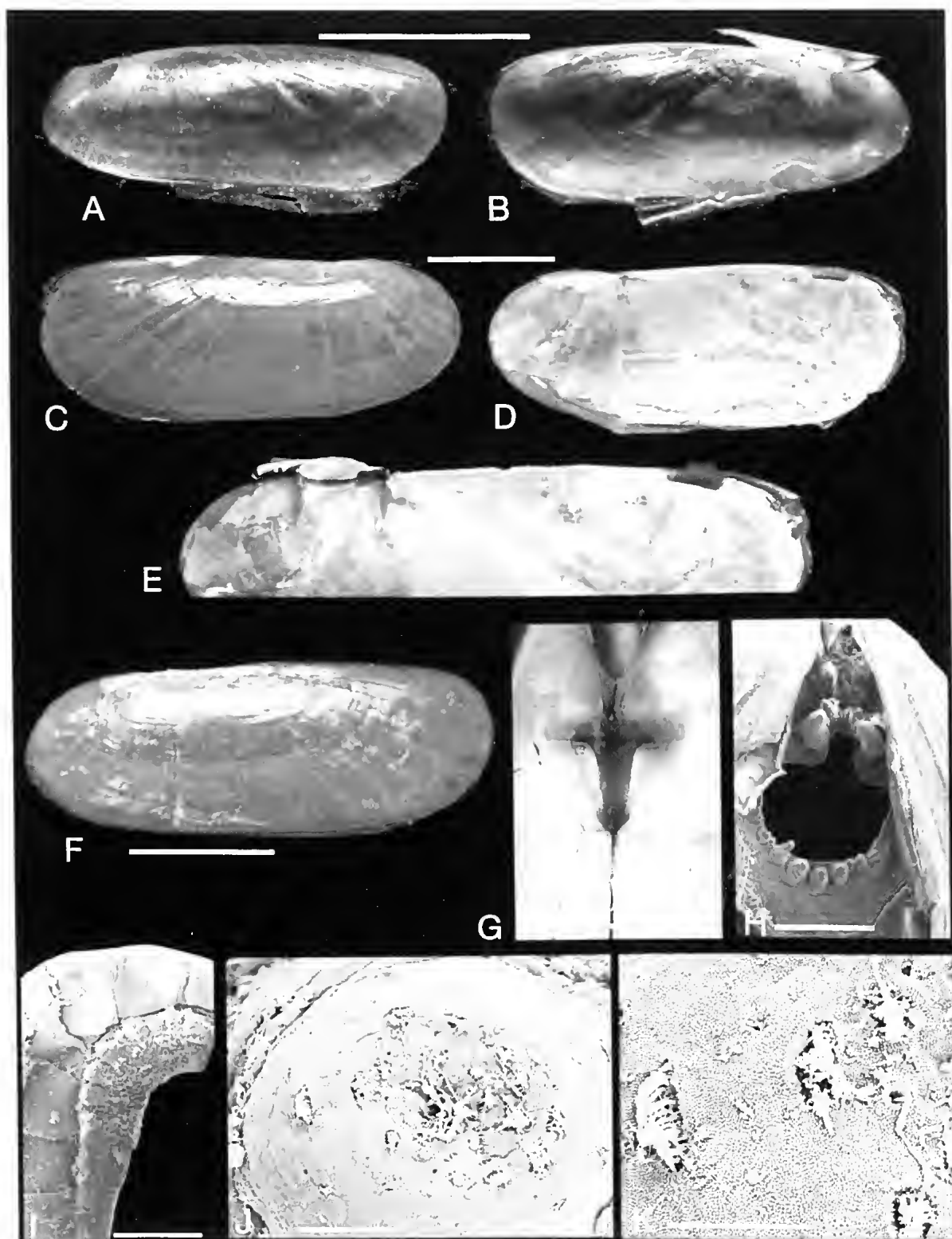
vietnamica Zorina, 1978 and *Anodontia omissa* (Iredale, 1930).

Remarks. Iredale (1931) introduced this species on the grounds that no large *S. australis*-like specimens are found in New South Wales and thus the smaller Sydney species was distinct. He gave no formal description or figure but stated that it differed from *S. terraereginae* in being "...more dilated anteriorly and more closely ribbed posteriorly". Note that Iredale introduced the species as *Solemya* on p. 201, but on p. 202 he named it as the type species of the new genus *Solemyarina*.

Solemya (Solemyarina) terraereginae
Iredale, 1929
(Figs 5A–G)

Solemya terraereginae Iredale, 1929: 262, pl. 30, fig. 13.
Solemyarina terraereginae – Iredale, 1939: 233.
Solemya (Solemyarina) velesiana – Lamprell & Healy, 1998: 42, fig. 49 (in our opinion this figured specimen (AMS C 150118) from Bowen, Central Queensland is *S. terraereginae*).

Material Examined. HOLOTYPE. One whole shell, Green I., Queensland (see Iredale 1939: 233) (AMS C 10074). Length 11.1 mm. OTHER MATERIAL. Queensland: Bowen (fig'd specimen in Lamprell & Healy as *S. velesiana*) (AMS C 150118); Innisfail, Kurramine Beach (AMS); Fraser I. (AMS); Swain Reef (AMS); 10-12 fathoms off Michaelmas Cay (AMS); Lizard I., Mangrove Beach (BMNH; AMS); Lady Musgrave I. (AMS C 150115, C 150117); Cooktown, Annan River Mouth (AMS); Great Palm I. (AMS); Torres Strait, S. side of Thursday I. (AMS).

Description. Shell small, length to 8 mm, dorsal and ventral shell margins sub-parallel, periostracum straw-coloured, with faint, evenly spaced rays. Internal ligament (Figs 5 C, E) with dorsal edges of chondrophore parallel and narrowly separated; posterior margin of chondrophore sinuate; anterior end of ligament enlarged into pads and anterior linear lateral extensions present. The aperture (Fig. 5F) has a single dorsal papilla, four pairs of short suprasiphonal papillae, with the largest of these ventral, and 8–9 short, siphonal papillae at the ventral margin.

Distribution. Queensland.

Habitat. At Lizard Island, Queensland, *S. (S.) terraereginae* occurred in lagoon sands (J.T & E.G. pers. observ.) with a sparse covering of the seagrass *Halophila* and in association with the lucinid bivalves *Anodontia ovum* (Reeve, 1850), *Chavania striata* (Tokunaga, 1906) and *Wallucina fijiensis* (Smith, 1885).

Remarks. This species is closely similar to *S. velesiana* but is smaller (length <8 mm), with a paler colour and less prominent radial ribs. The ligament is similar in both species but in *S. terraereginae* the posterior edge of the chondrophore is sinuous rather than straight as in *S. velesiana*. In anatomical characters the gill filaments are much thinner in *S. terraereginae* (9–12 mm compared to 18–20 mm of *S. velesiana*) see also Kreuger & Cavanaugh 1997, fig. 2). The arrangement of papillae around the posterior aperture is similar in both species.

Solemya terraereginae was synonymised with the southern Australian species, *S. australis*, by Lamprell & Healy (1998) and in the Database of Indo-Pacific Marine Molluscs (http://data.acnatsci.org/obis/search.php) but comparison with the type material shows that this is incorrect (compare Figs 3 & 5).

Solemya (s.l.) moretonensis sp. nov.
(Figs 6A–G)

Material Examined. HOLOTYPE. One whole shell, length 5.4 mm, Moreton Bay, north end of Moreton I., Queensland, 26° 56.60' S, 153° 24.25' E, 31 m. (QM-Mo74208); PARATYPES: same locality: one preserved animal (Fig. 6C, BMNH-20060153); one dry shell Fig 6E (QM-Mo74209). F. one animal dried (Fig. 6F, BMNH-20060154); two preserved animals (QM-Mo74210; four dry shells (BMNH-20060155); one preserved animal and three valves (BMNH-20060156).

Description. Shell small, fragile, length to 6.6 mm, shell and periostracum transparent to slightly yellowish. Faint radial ribs visible anteriorly and posteriorly. Ligament with dorsal margins of chondrophore diverging; posterior

◀ FIG. 4. A–K. *Solemya (Solemyarina) velesiana* (Iredale, 1931). A–B, holotype, exterior and interior of right valve (AMS C7476); C–E, exterior and interior of left valve and detail of ligament, Middle Harbour, Port Jackson, Sydney (BMNH 95.3.7.17-19); F, Moreton Bay (BMNH), G, detail of ligament, Moreton Bay (BMNH); H, posterior aperture, Moreton Bay (BMNH); I, papillae at dorsal edge of pedal gape; J, tip of siphonal papilla with ciliary tufts; K, detail of I with single cilia and groups of cilia arising from small pits. Scale bars: A,B,C,D = 5 mm; G = 2 mm; H = 500 μm; I = 250 μm; J = 20 μm; K = 5 μm.
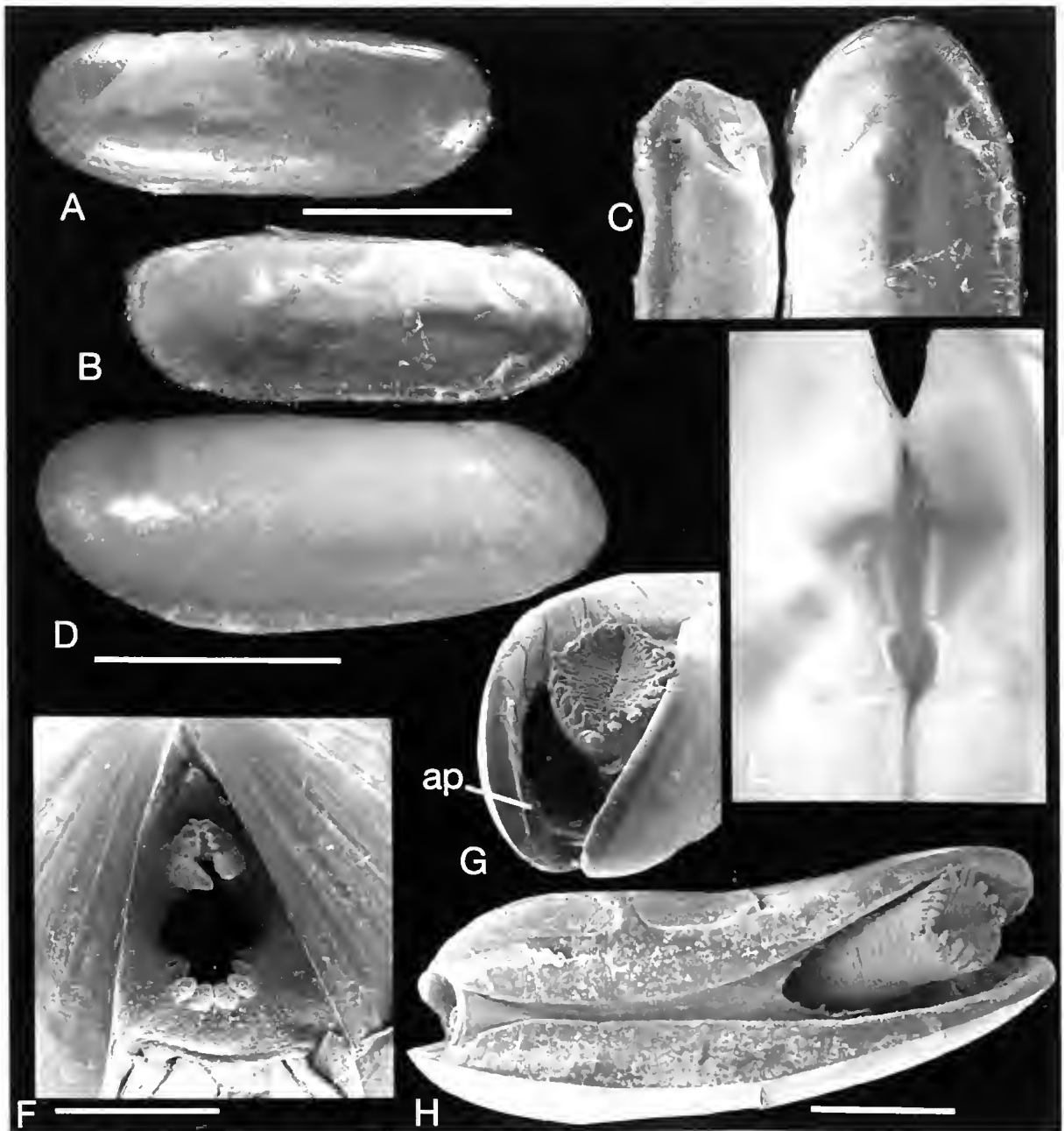
FIG. 5. *Solemya* (*Solemyarina*) *terraereginae* (Iredale, 1929). **A–C**, Holotype, exterior, interior and detail of ligamental area, Green Island, Queensland (AMS C 10074); **D–G**, Mangrove Beach, Lizard Island, Queensland; **D**, left side of preserved animal (BMNH); **E**, internal view of ligamental area; **F**, posterior aperture; **G**, anterior view showing anterior papilla in pedal gape; **H**, ventral view showing pedal gape and mantle fusion. ap = anterior papillae. Scale bars: A,B,C,D = 5 mm; F = 500 µm; G = 2 mm.
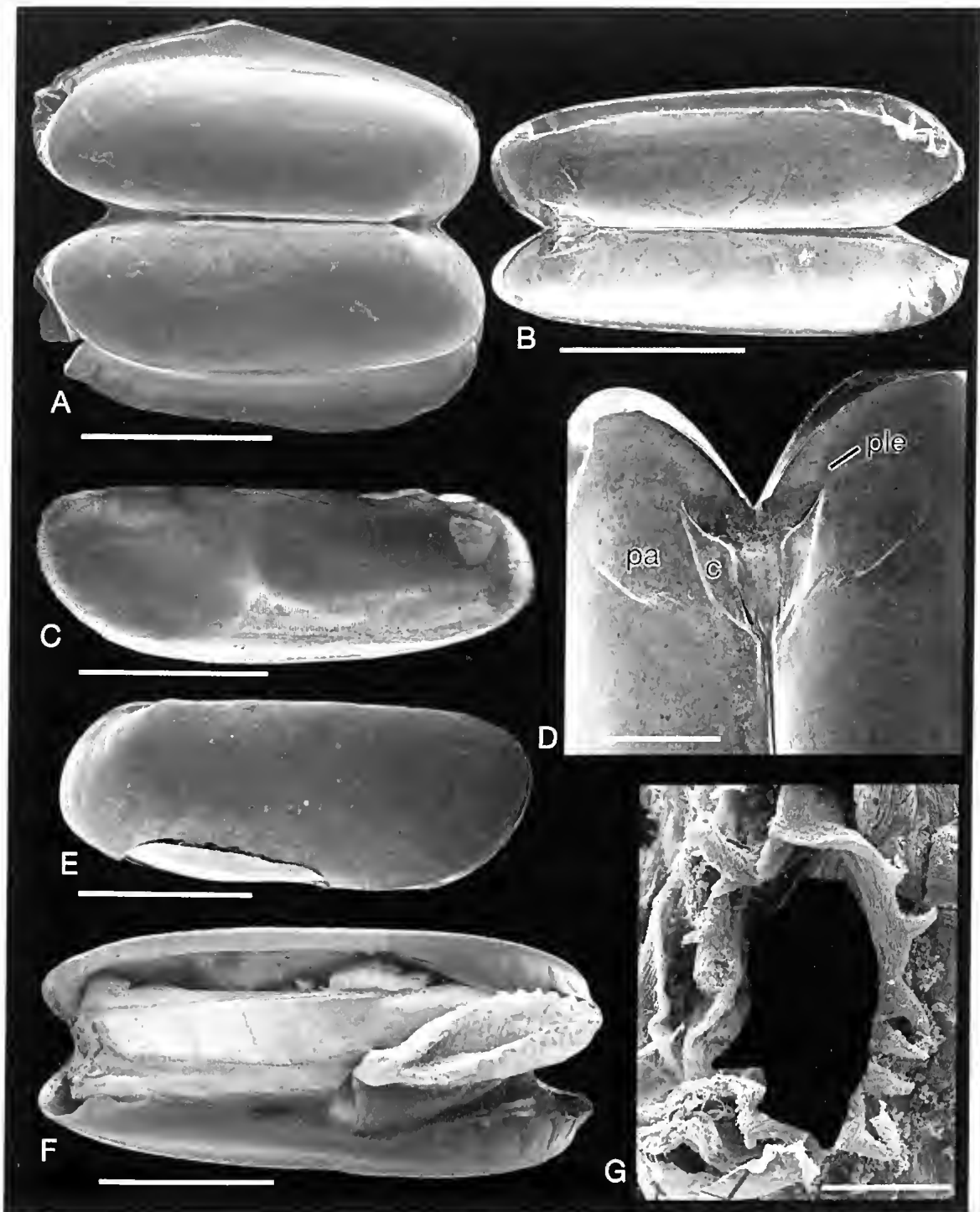
FIG. 6. *Solemya* (s.l.) *moretonensis* sp. nov. **A**, Holotype (QM-Mo74208) exterior of valves; **B**, ventral view of valves; **C**, paratype (BMNH-20060153) lateral view left valve; **D**, holotype detail of ligamental area; **E**, paratype (QM-Mo74209) right side; **F**, paratype (BMNH 20060154) ventral view; **G**, posterior aperture. c = chondrophore; pa = posterior adductor scar; ple = posterior ligament extension. Scale bars: A, B, C, E = 2 mm; D = 500 μm; F = 1 mm; G = 200 μm.
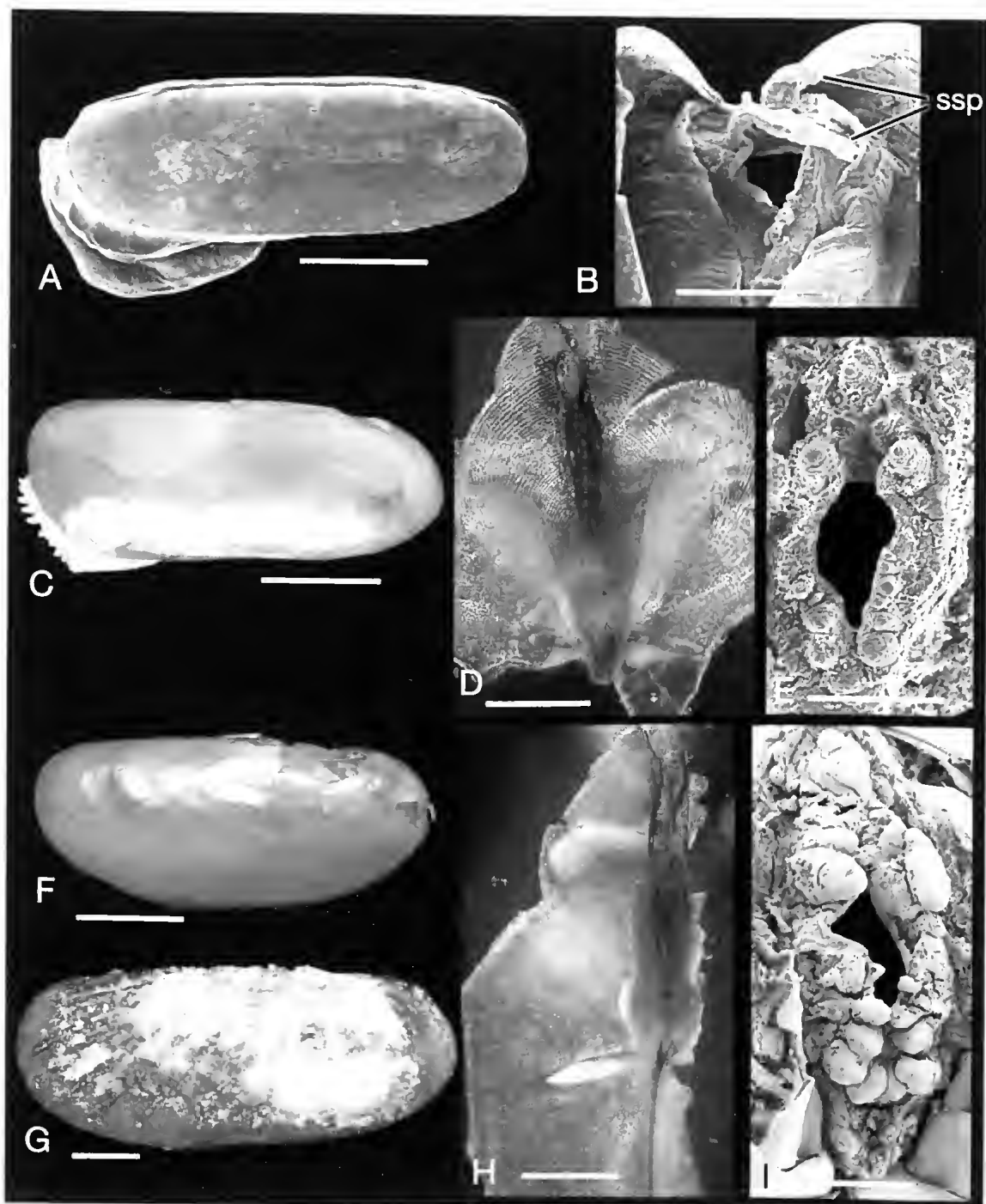
FIG. 7. Other small Solemyidae from Moreton Bay, Victor Harbor, South Australia and Shark Bay, Western Australia. A–B, *Solemya* sp. Banana Bank, Moreton Bay, Queensland. A, exterior of shell from left side; B, posterior aperture; C-E, *S. (Solemyarina)* species A. Victor Harbour, South Australia; C, external of shell left side; D, internal ligament; E, posterior aperture. F-I, *S. (Solemyarina)* species B. Little Lagoon, Denham, Shark Bay, Western Australia; F, exterior shell; G, another specimen corroded by fixative; H, ligamental area; I, posterior aperture. ssp = suprasiphonal papillae. Scale bars: A, C, F, G = 2 mm; B, E = 500 µm; D, H, I = 1 mm.

dorsal edge of chondrophore projected as a pointed ridge (Fig. 6D). Chondrophoral ridge around the adductor scar slight. Posterior adductor scar does not extend behind chondrophore. Anterior lateral extensions of ligament absent. Posterior margin of outer ligament with small tongue-like extensions (Fig. 6D ple). The posterior aperture (Fig. 6G) is not well preserved but appears to have some suprasiphonal papillae; the most ventral of these is very long. Siphonal papillae probably extend around the apertural margin with likely 12–14 in total.

Remarks. From external characters, this small species might be considered as a juvenile of *S. velesiana*, but the structure of the ligament differs in lacking anterior lateral extensions, the resilium is broad and triangular and the posterior ends of the chondrophore are pointed. Additionally, the siphonal papillae are longer and seem to extend around the aperture rather than grouped ventrally as in *S. velesiana*. The generic placement of this species is uncertain but the ligament, chondrophore and resilium resemble the New Zealand species *S. (Zesolemya) parkinsonii*, although it lacks the anterior, linear, lateral ligament extensions of that species.

Solemya (s.l.) undescribed species
(Figs 7A, B)

Material Examined. A single specimen, shell length 7.3 mm, from mud, Banana Bank, southern Moreton Bay, 26°56.6'S, 153°24.25' E (BMNH-20060159)

Remarks. In addition to *S. velesiana* and *S. moretonensis* from Moreton Bay, we have a single specimen of a third species. Although similar to *S. velesiana* in external shell characters, the posterior aperture differs in having a pair of long suprasiphonal papillae (Fig 7B) and short siphonal papillae. The internal ligament also lacks anterior lateral extensions. The characters of the posterior aperture with the long pair of suprasiphonal papillae are more similar to *Solemya* and *Petrasma* species (see Fig 2 A,B) than to *Solemyarina*. Further sampling of solemyids in Moreton Bay should reveal more details of this species

In addition to the species described above we recognise two other taxa based on molecular data and some morphological characters but we have insufficient well- preserved material of these for formal descriptions in this paper. Specimens were cracked and fixed in the field in 100 % ethanol for molecular analysis and, as a result, some of the diagnostic morphology such as the posterior apertures are poorly preserved. On the basis of ligament characters we would include them within the concept of *Solemyarina*; *Solemyarina* sp. A from Victor Harbor, South Australia and *Solemyarina* sp. B from Shark Bay, Western Australia.

Solemya (Solemyarina) species A
(Figs 7C, D, E)

Material Examined. Eight individuals — one complete animal and remainder with shells cracked or dissected, Anchorage Bay, Victor Harbor, South Australia (BMNH-20060150).

Description. Shell small, length to 7.3 mm, thin shelled, pale brown to fawn with faint white rays, to anterior and posterior. Chondrophore margins widely spaced with a triangular resilium. The posterior margin of chondrophore is more or less straight. Chondrophoral buttress slight. Anterior lateral extensions of ligament are short and narrow. On the only specimen where the posterior aperture was visible it is similar to *S. velesiana* but there appear to be more siphonal papillae (Fig. 7E).

Habitat. Collected from thin, muddy sand on intertidal rock platform with *Heterozostera*, *Posidonia australis* and *Amphibolis*. The solemyids occurred in association with the lucinid bivalves, *Epicodakia tatei* (Angas, 1879), *Notomyrtea ada* (Adams & Angas, 1863) and *Anodontia perplexa* (Cotton & Godfrey,1938).

Remarks. This species occurs within the geographical range of *S. (Austrosolemya) australis* but differs in size, colour and form of ligament.

Molecular evidence from sequences of the cytochrome B gene (Table 2) indicates that this species is distinct from both *S. (Solemyarina) velesiana* from Moreton Bay and *S. (S.) sp. B from Shark Bay by 17% & 19% (Kimura distance) respectively.

Solemya (Solemyarina) species B
(Figs 7F–I)

Material Examined. Three individuals (two dissected), lengths 11.9–12.4 mm, Little Lagoon, Denham, Shark Bay, Western Australia, mud and
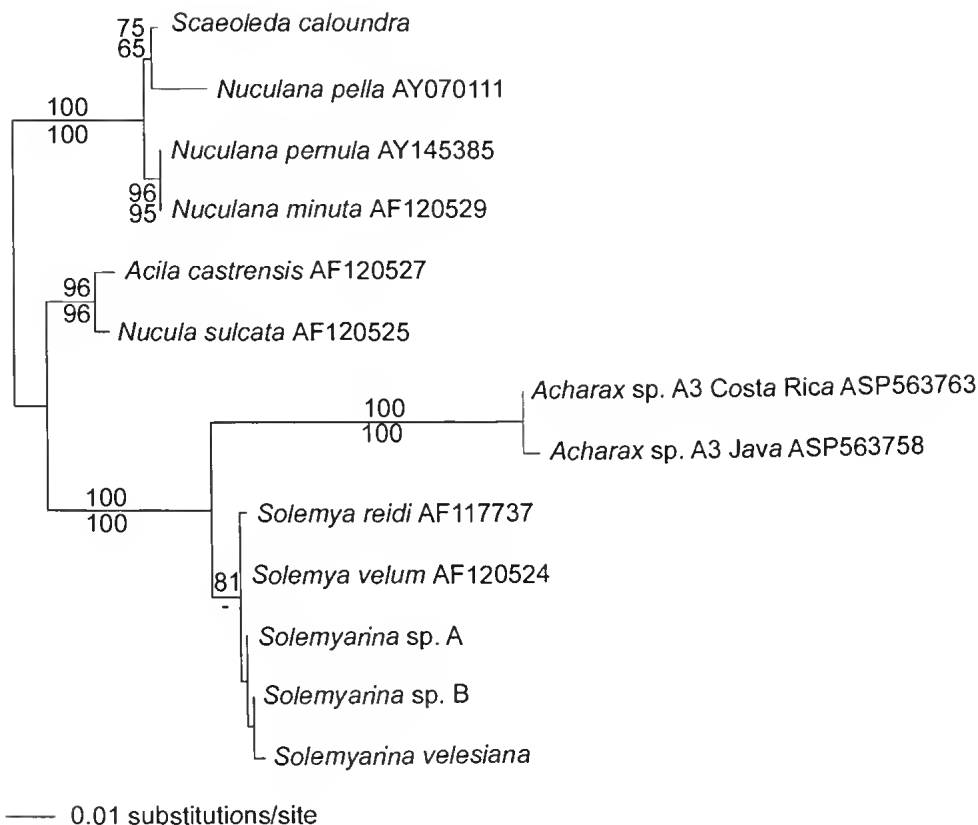
18S
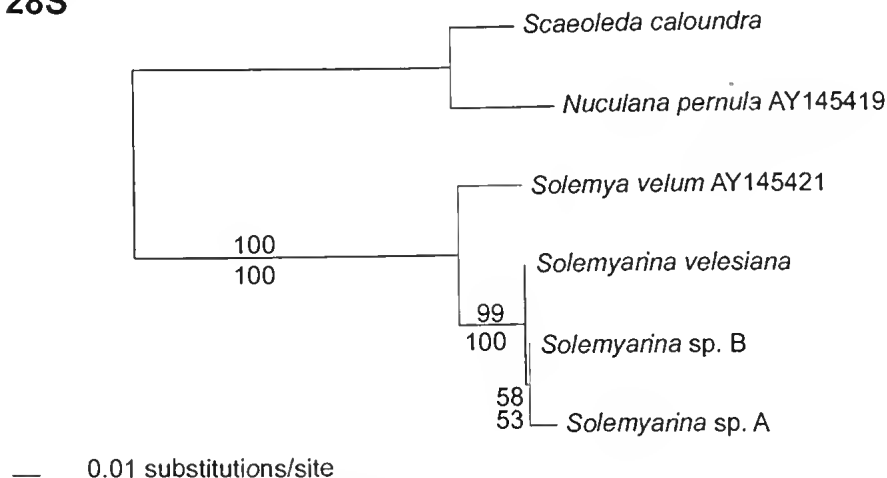
FIG. 8. Molecular phylogenies for single gene analyses of 18S rRNA and 28S rRNA genes produced by maximum likelihood analyses. *Scaeoleda* and *Nuculana* (Nuculanidae) were drawn as the outgroup. Nodal support above branches is based on maximum likelihood (ML) bootstrap values and below branches, neighbour joining using ML distances.

Table 1. List of species used in the molecular analysis with voucher and GenBank accession numbers. Full details are given for the new analyses reported in this study.

Species	Location	Voucher reg no	18S	28S	Cyt B
Nuculidae					
Nucula sulcata Bronn, 1831			AF120525		
Acila castrensis (Hinds, 1843)			AF120527		
Nuculanidae					
Nuculana minuta (Müller, 1776)			AF120529		
Nuculana pella (Linnaeus, 1767)			AY070111		
Nuculana pernula (Müller, 1779)			AY145385	AY145421	
Scaeloleda caloundra (Iredale, 1929)	Moreton Bay, Qld	BMNH 20060149	AM293663	AM293664	
Solemyidae					
Acharax sp. Costa Rica			ASP563763		
Acharax sp. Java			ASP563758		
Solemya reidi Bernard, 1980			AF117737		
Solemya velum Say, 1822			AF120524	AY145421	
Solemyarina velesiana (Iredale, 1931)	Moreton Bay, Qld	BMNH 20060151	AM293669	AM293668	AM293670
Solemyarina sp. A	Victor Harbor, SA	BMNH 20060150	AM293666	AM293667	AM293665
Solemyarina sp. B	Denham, Shark Bay, WA	BMNH 20060152	AM293672	AM293673	AM293671

Table 2. Kimura 2-parameter distance matrix for cytochrome B sequences.

	1	2
Solemyarina A (Victor Harbor)	-	
Solemyarina B (Shark Bay)	0.196	
Solemyarina velesiana (Moreton Bay)	0.174	0.097

dead algae in mangrove channel (BMNH-20060152 molecular voucher; BMNH-20060160).

Description. Small, length to 12.4 mm, yellow brown with slightly raised pale rays. Ligament with chondrophore margins not widely separated, heart-shaped anterior area with narrow anterior extensions of the ligament at 90° to shell margin. Posterior margin of chondrophore sinuate. Posterior aperture with prominent suprasiphonal and large siphonal papillae around the ventral margin of the aperture.

Remarks. Characters of the ligament, chondrophore shape and anterior lateral extensions are most similar to *S. (S.) terraereginae* from Queensland, but the posterior aperture of the Shark Bay species has larger siphonal and suprasiphonal papillae. Molecular evidence from cytochrome B sequences shows that this species is separated from *S. (S.) velesiana* from Moreton Bay by 9.8% (Kimura distance).

MOLECULAR ANALYSIS

Sequences from 18S rRNA and 28S rRNA and cytochrome B genes were obtained from three species: *S. (Solemyarina) velesiana* from Moreton
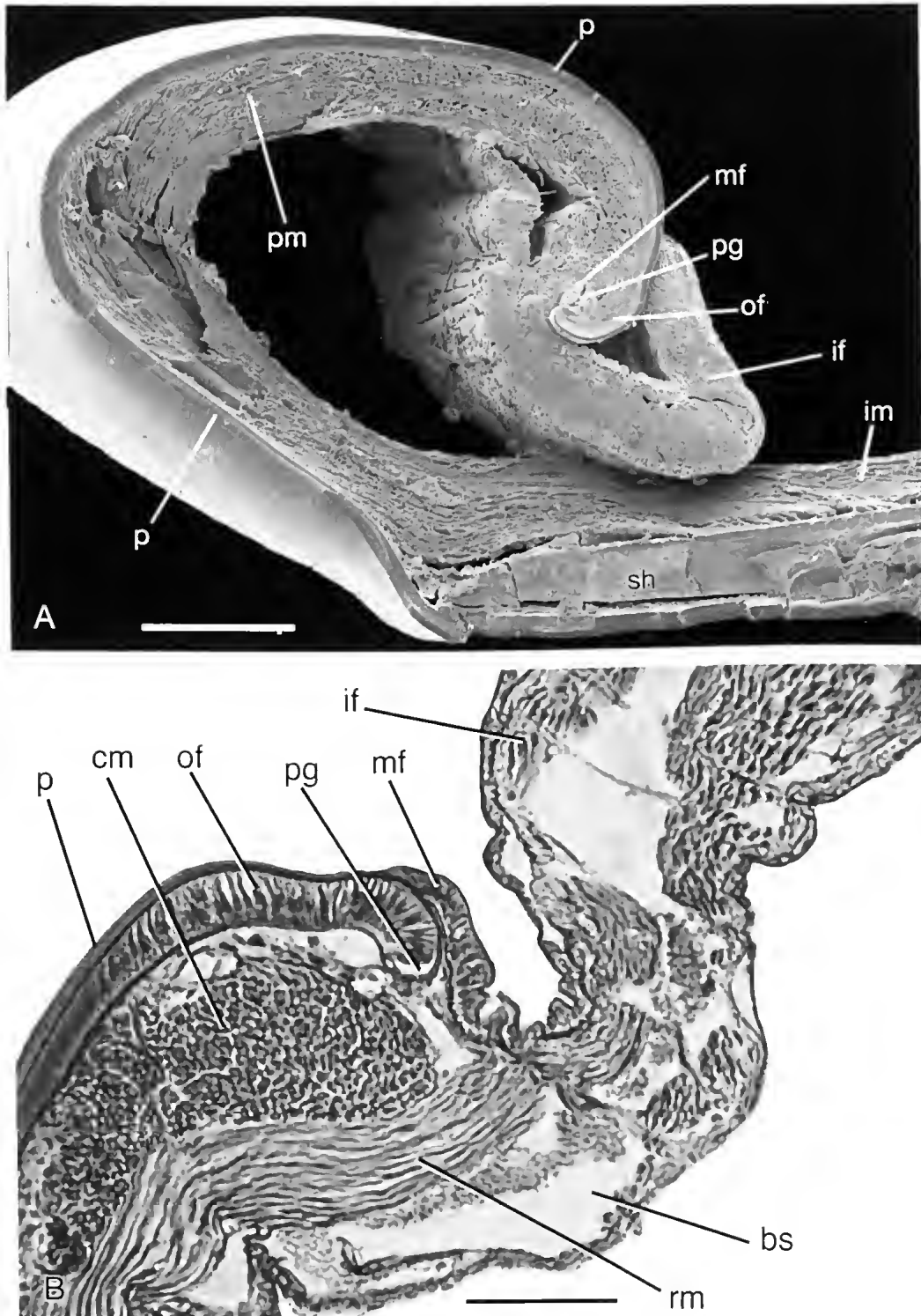
FIG. 9. Mantle margin of *Solemya* (*Solemyarina*) *velesiana*. **A**, cut shell edge and mantle margin; **B**, thin section of mantle edge to show mantle folds and periostracal groove. Scale bars: A = 200 μm; B =100 μm. bs = blood space; cm = circular muscle; if = inner mantle fold; im = inner mantle; mf = middle mantle fold; of = outer mantle fold; p = periostracum; pg = periostracal groove; pm = pallial muscles; rm = radial muscles; sh = shell.
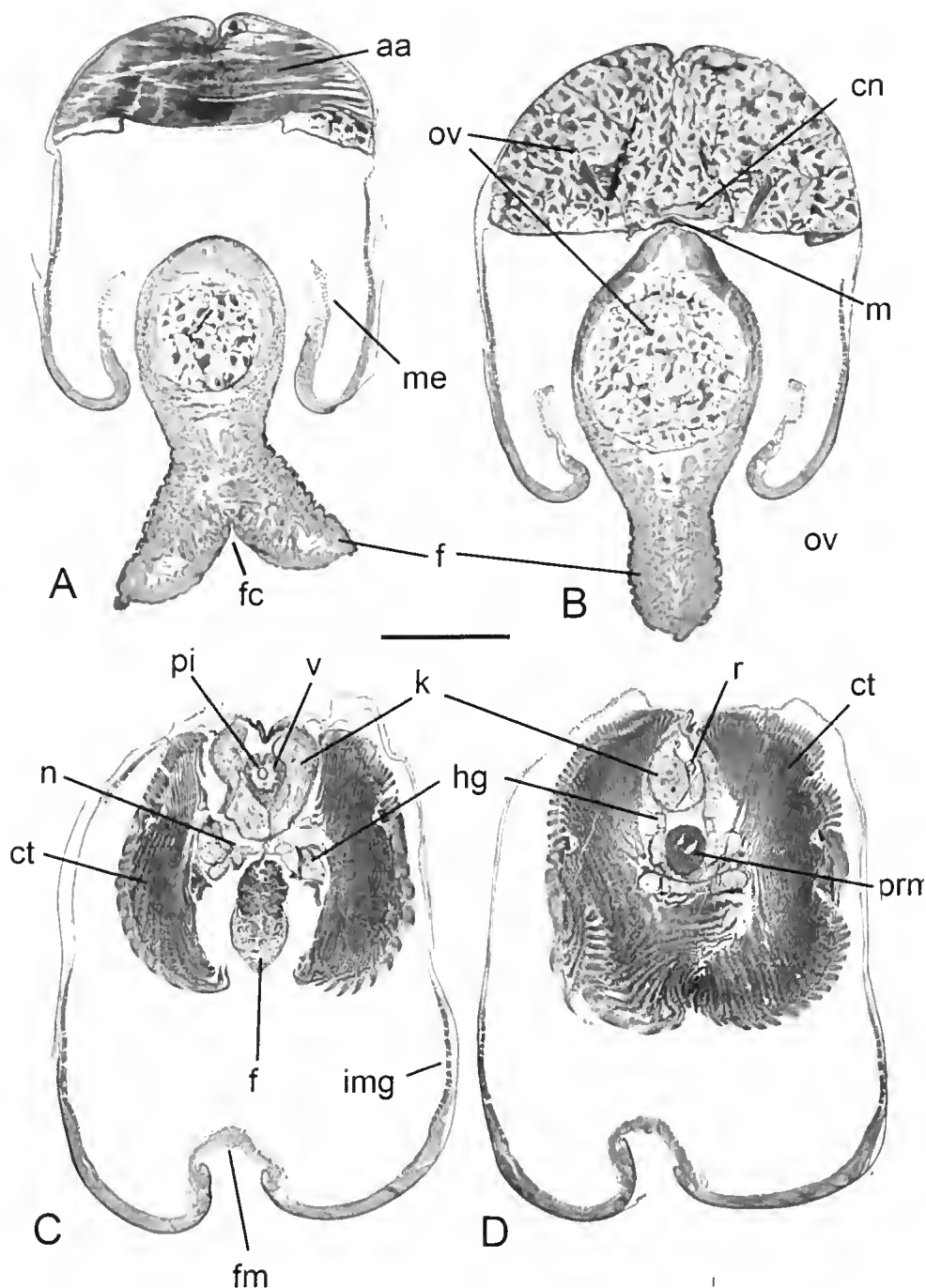
FIG. 10. A–D. four sections from anterior to posterior through body of *Solemya (Solemyarina) velesiana* from Moreton Bay. **A**, anterior section through anterior adductor muscle and foot; **B**, section through mouth with ovary and foot; **C**, section around midline through ventricle and ctenidia; **D**, posterior section through ctenidia and hypobranchial gland. Scale bar = 1.0 mm. aa = anterior adductor muscle; cn = circum-oral nerve; ct = ctenidium; f = foot; fc = foot cleft; fm = fused mantle; hg = hypobranchial gland; k = kidney; l = ligament; m= mouth; me = mantle edge; img = inner mantle gland; n = nerve; ov = ovary; pe = periostracum; pi = posterior intestine; prm = pedal retractor muscle; r = rectum, v = ventricle.
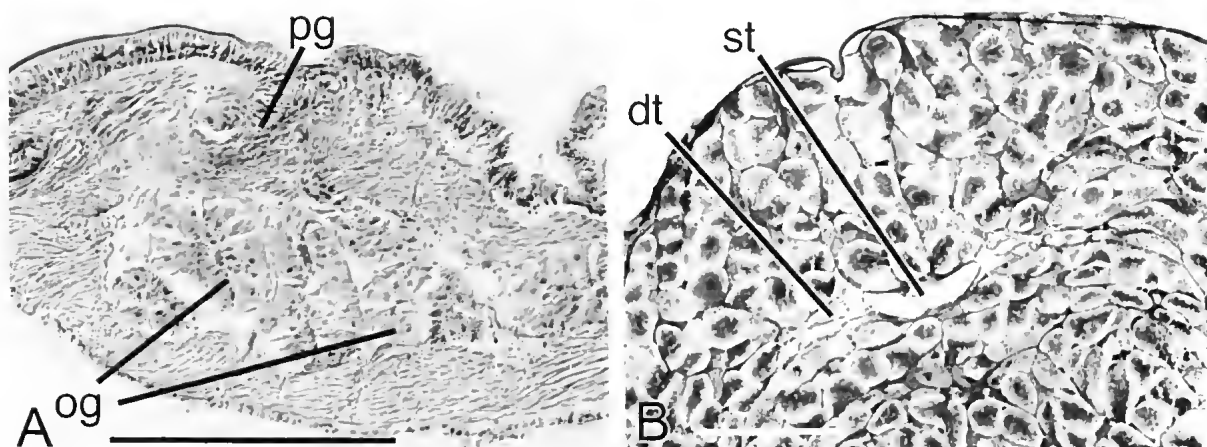
FIG. 11. *Solemya (Solemyarina) velesiana*. **A**, section of anterior mantle with tubular "oil glands"; **B**, section through ovary and stomach. Scale bars: A= 200 μm; B = 500 μm. dt digestive tubules; og = oil glands; pg = periostracal groove; st = stomach.

Bay, S. (*Solemyarina*) sp. A from Victor Harbor and S. (*Solemyarina*) sp. B from Shark Bay. Unfortunately, we failed to extract and amplify DNA from the S. (*Solemyarina*) *terraereginae* samples from Lizard Island and no suitably preserved specimens of S. (*Austrosolemya*) *australis* and S. *moretonensis* were available for analysis. Additionally, sequences of other Solemyidae obtained from GenBank were included in the analysis - two species of *Acharax* (Neulinger *et al*, 2006), *Solemya (Petrasma) velum* and S. *reidi*. The sequence data for *Solemya togata* lodged in GenBank has anomalous features and was not used in our analysis. These solemyids were compared with other protobranch bivalves as outgroups, namely four species of Nuculanidae and two species of Nuculidae. All new sequences have been deposited in GenBank (Table 1).

A single maximum likelihood tree was obtained for 18S rRNA (-ln L = 2094.184) and for 28S rRNA (-ln L = 3465.939) (Fig. 8). Sequences for more taxa were available for 18S rRNA so the two trees are not directly comparable, although there are no significant incongruencies. In the 18S tree (Fig 8A) the Solemyidae, including *Acharax*, form a well-supported clade, with *Acharax* forming a sister clade to the shallow water *Solemya* species. The results also indicate Solemyidae are more closely related to Nuculidae than Nuculanidae.

In the 28S rRNA tree the three Australian species form a well-supported clade distinct from *Solemya (Petrasma) velum* from eastern America but this is less well supported in the 18S tree. Relationships between Australian species are poorly supported. Sequences from the cytochrome B gene gave better resolution of relationships amongst these species. Distance estimates (Table 2) based on a single sequence for each species (Kimura 2-parameter (Kimura 1980)) suggested that the S. (*Solemyarina*) sp. B from Shark Bay is more closely related to S. *Solemyarina velesiana* from Moreton Bay (9.8%) than either are to S. (*Solemyarina*) sp. A from Victor Harbor (Sol. A: Sol. veles =17.5%; Sol. A: Sol. B =19.7%). These distances are well above the cut-off values normally indicative of separate species.

MORPHOLOGY OF *S. (SOLEMYARINA) VELESIANA*

Very few solemyid species, particularly those from the Indo-West Pacific, have been documented in any detail and in this section we describe and illustrate some major features of the anatomy of *Solemya (Solemyarina) velesiana* from Moreton Bay. We also studied the anatomy of S. (*S.*) *terraereginae* that is similar in most respects, except for the thickness of the ctenidial lamellae and bacteriocytes.

MANTLE FUSION AND APERTURES

The mantle is fused along the entire posterior half of the ventral margin with a large anterior pedal gape and a single aperture to the posterior. The ventral edges of the mantle surrounding the pedal gape bear a few short
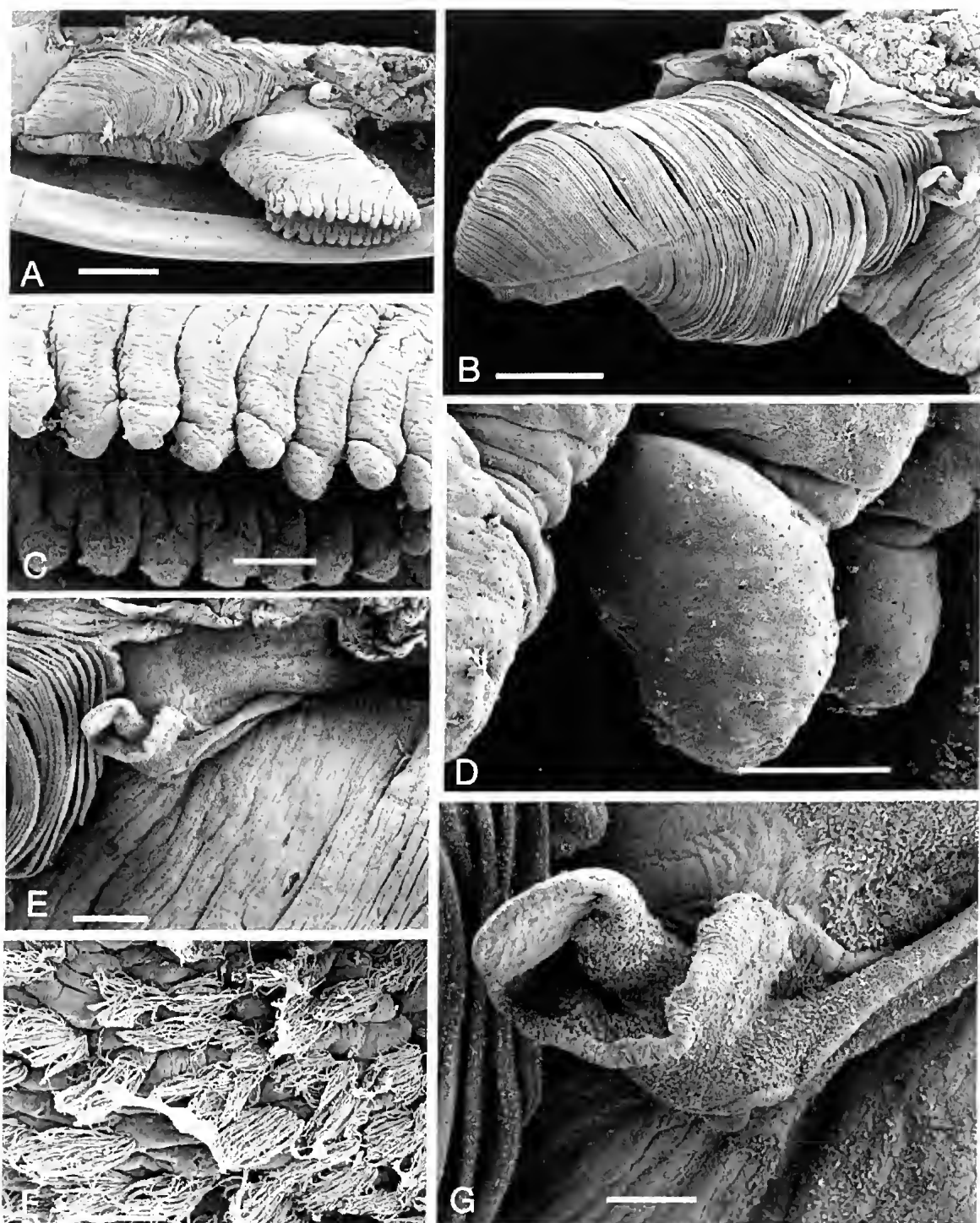
FIG. 12. *Solemya (Solemyarina) velesiana* Moreton Bay, details of anatomy. A, right valve and mantle removed to show foot, ctenidium and palp proboscis, scale bar = 1 mm; B, right ctenidium, scale bar = 1 mm; C, detail of foot showing papillate fringe, scale bar = 200 μm; D, detail of tip of foot papilla, note pores, scale bar = 50 μm; E, palp proboscis and groove leading to mouth, scale bar = 500 μm; F, ciliary tufts on surface of palp, scale bar = 20 μm; G, detail of distal end of palp with surface of ciliary tufts, scale bar = 200 μm.
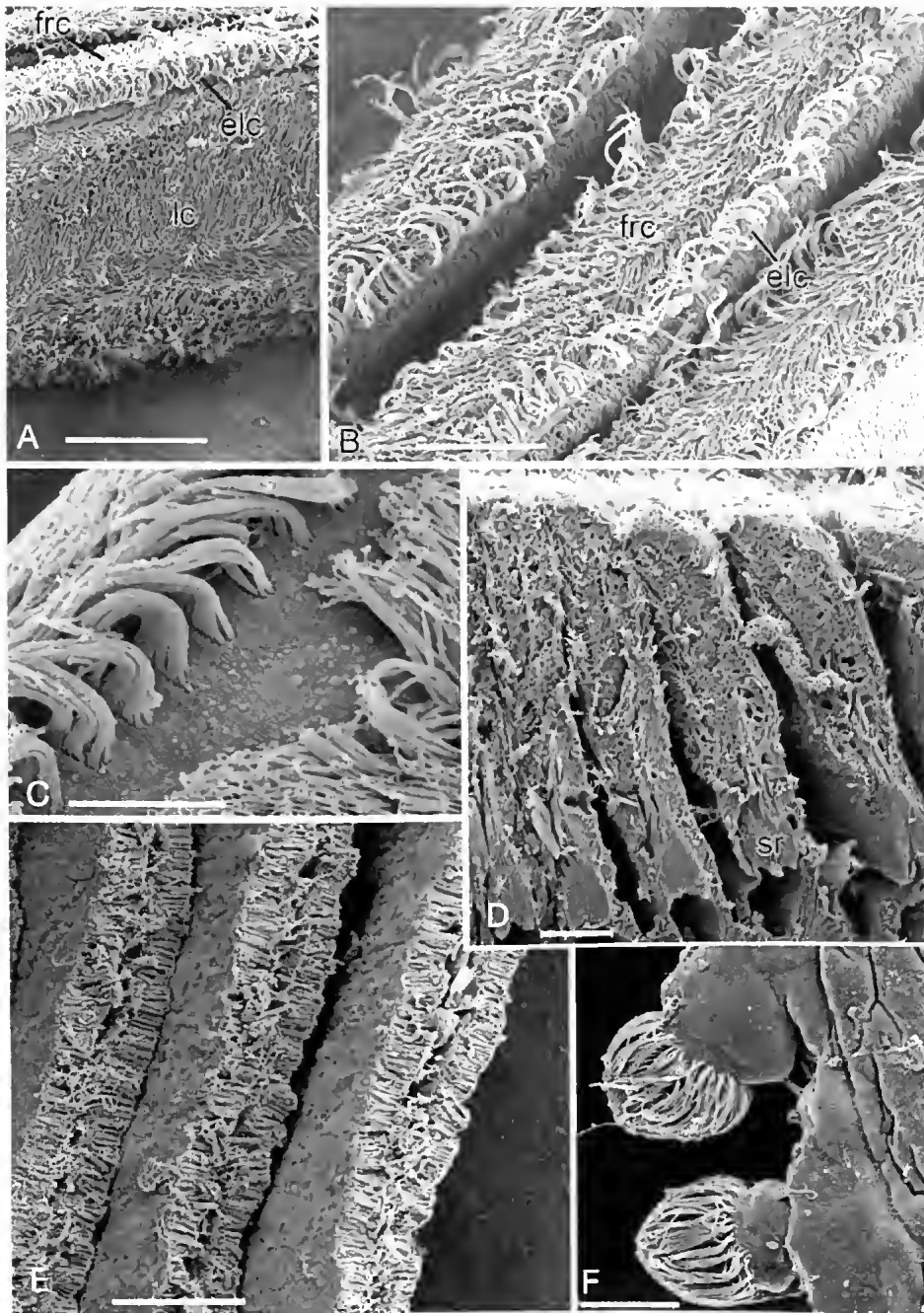
FIG. 13. A–F. *Solemya (Solemyarina) velesiana* Moreton Bay, details of ctenidia. **A**, lateral view of outer portion of gill lamella with band of lateral cilia and eulatero-frontal and frontal cilia. scale bar = 50 μm; **B**, outer edge of lamella showing eulaterofrontal and frontal cilia, scale bar = 20 μm. **C**, bases of eulatero-frontal cilia, scale bar = 5 μm; **D**, transverse sections through distal ends of several lamellae showing supporting rods, scale bar = 20 μm; **E**, sections through three adjacent lamellae packed with bacteria, scale bar = 20 μm; **F**, ciliated tufts (ciliated knobs of Yonge 1939) from abfrontal edge of gill lamellae, scale bar =10 μm. frc = frontal cilia, elc = eulatero-frontal cilia; lc = lateral cilia; sr = supporting rod.
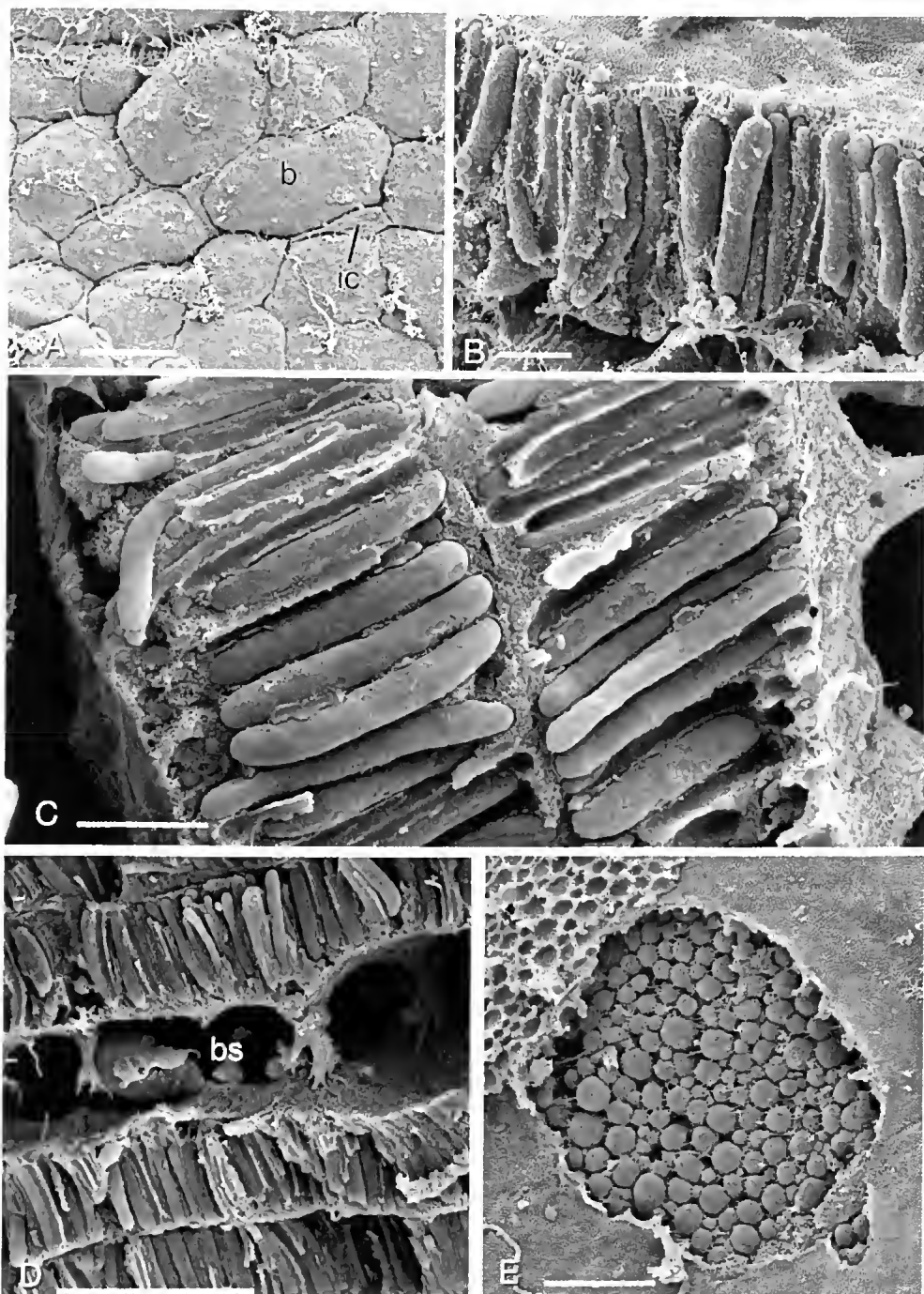
FIG. 14. *Solemya* (*Solemyarina*) *velesiana* Moreton Bay, details of bacteriocytes. **A**, surface of gill lamella showing outer surfaces of bacteriocytes and intercalary cells, scale bar = 10 µm; **B**, section of lamella with bacteria aligned vertically in bacteriocytes beneath the microvillli, scale bar = 2 µm; **C**, two adjacent gill lamellae with aligned bacteria, scale bar = 2 µm; **D**, central blood space between sheets of bacteriocytes, scale bar = 10 µm; **E**, surface of bacteriocyte peeled back to show tips of bacteria packed within, scale bar = 5 µm. b = bacteriocyte; bs = blood space; ic = intercalary cell.
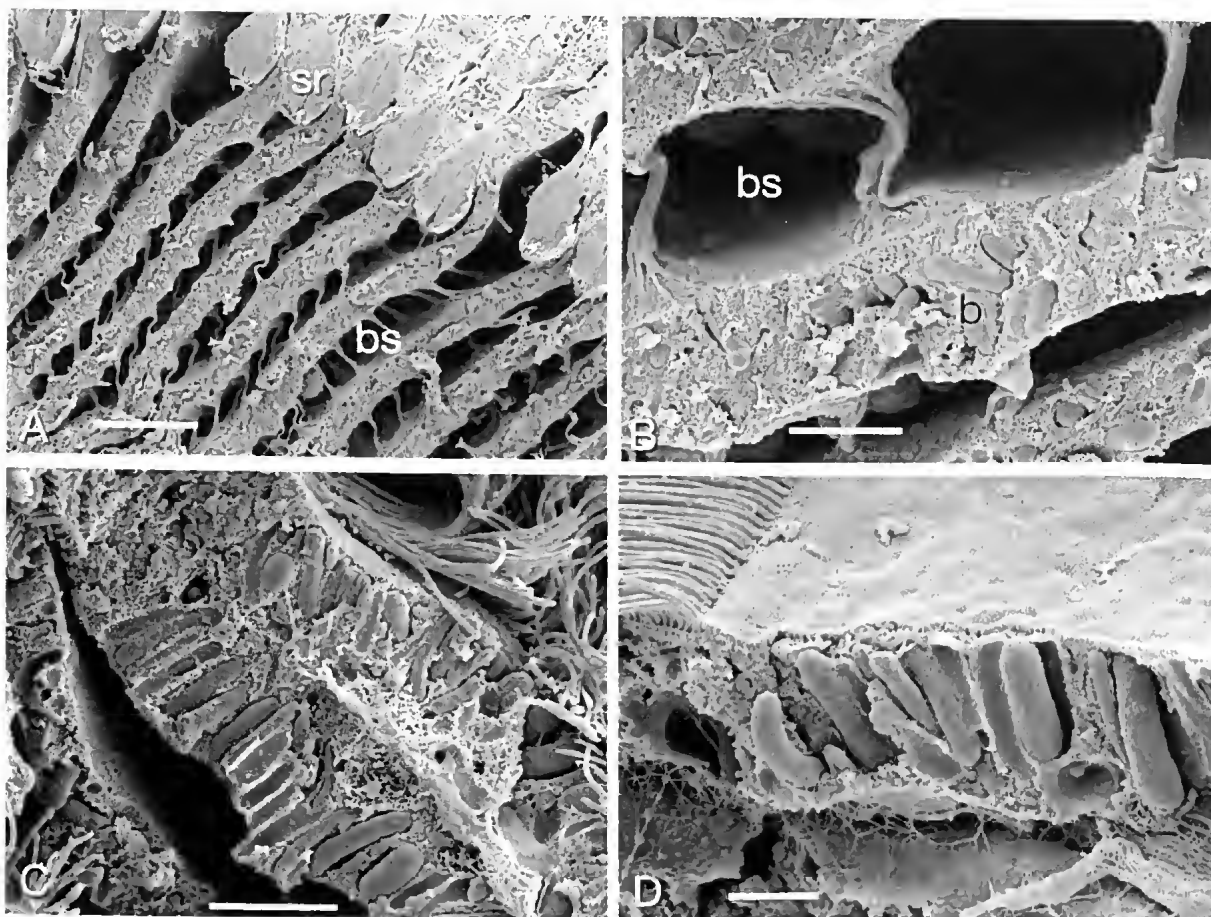
FIG. 15. Details of ctenidia of *Solemya* (*Solemyarina*) *terraereginae* Lizard Island. **A**, section through several gill lamellae scale bar = 20 μm; **B**, detail of lamellae and blood space, scale bar = 5 μm; **C**, first bacteriocytes in gill lamella, scale bar = 5 μm; **D**, detail of bacteria beneath microvilli, scale bar =2 μm; b= bacteria; bs = blood space; sr supporting rods.

papillae, with larger, stubby papillae at the antero-dorsal margins of the pedal gape. The posterior aperture possesses two sets of papillae; there are nine to ten siphonal papillae around the ventral margin decreasing in size laterally. On each side of the dorsal edge of the aperture there are four suprasiphonal papillae and above these a single dorsal papilla (Fig. 4H). The siphonal papillae have two types of putative sensory structures at their tips; either with single long cilia, or pits with groups of ca 20 short, stiff cilia (Fig. 4 I, J).

The mantle margin is thick and muscular with three folds; a large outer fold, a small, thin middle fold and a large and muscular inner fold (Fig. 9). Mantle fusion along the ventral margin of *Solemya* involves only the inner fold

(Fig. 10). One of the more remarkable features of all solemyids is the broad, marginal periostracal fringe. The periostracum arises in a narrow groove between the outer and middle folds, with the outer surface of the middle fold tightly appressed to it (Fig. 9B). The periostracum gradually thickens (to ca 25 μm) around the outer surface of the outer mantle fold and three distinct layers are visible from differential staining. A complex system of radial muscles ("orbicular" muscles of Beedham & Owen, 1965) occupies the periostracal fringe (Fig. 9A). Some of these extend from the mantle within the calcified shell into the periostracal fringe, others cross-connect the periostracum within the fringe, while others extend into the folds of the mantle margin. The inner mantle
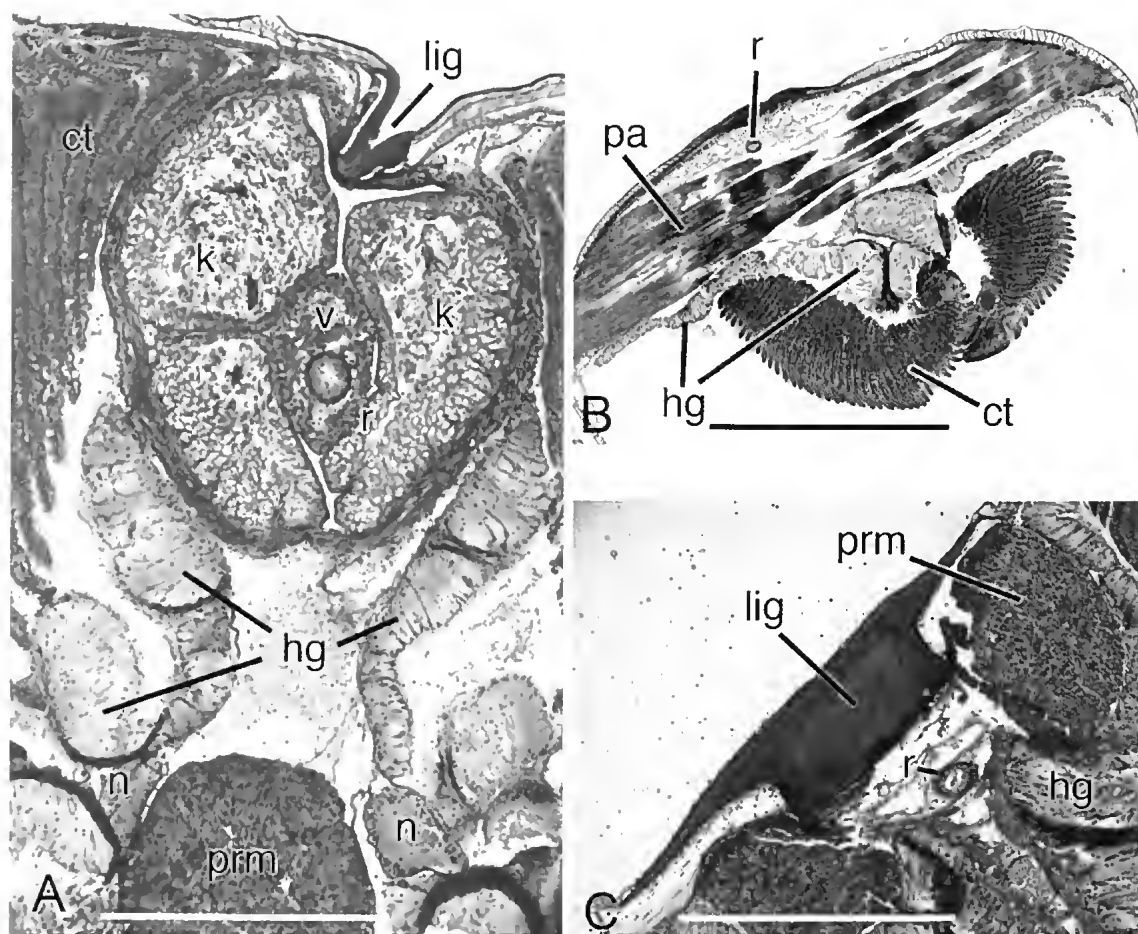
FIG. 16. Histological sections through *Solemya (Solemyarina) velesiana*, Moreton Bay. **A**, section through posterior of *S. velesiana* showing extensive hypobranchial gland and ventricle; **B**, section through posterior showing hypobranchial gland on inner mantle; **C**, section through posterior ligament resilifer. Scale bars: A,B,C = 500 μm. ct = ctenidia; hg = hypobranchial gland k = kidney; lig = ligament; n = nerve; pe = pericardium; prm = pedal retractor muscle; r = rectum; v= ventricle.

fold is also highly muscular, with bundles of circum-pallial muscles as well as radial and transverse muscles. Calcification on the inner surface of the periostracum commences around 2 mm from the mantle margin and comprises an outer layer of irregular "prisms" with thick organic boundaries between the prisms and a thin, inner layer of homogeneous/platy crystals.

The anterior and posterior mantle margins have distinctive tubular glands, the so-called oil glands of Beedham & Owen (1965). These glands, located in the proximal part of the inner mantle, open into the groove between the inner and middle mantle folds (Fig. 11A). It has been suggested (Yonge, 1939; Beedham & Owen, 1965) that the glands secrete a lipo-protein responsible for the water-repellant properties of the periostracum. Away from the margins, the mantle is very thin, with a low, cuboid, outer epithelium but ventrally, the inner epithelium is glandular with tall glandular cells staining orange-red. This glandular area was called the anterior pallial organ by Stempell (1899) but not mentioned by Yonge (1939) or Beedham & Owen (1965). The function of this gland is uninvestigated.

FOOT

S. (Solemyarina) velesiana has a large foot with a deep central cleft, and is highly extensible, as in most solemyids. The foot is fringed with around 28 papillate projections with differentiated tips (Fig. 12A, C). Numerous small

pores (1–2 μm diameter) open to the surface of the papillae (Fig. 12D). In section, the foot is highly muscular with a small, narrow pedal gland opening into the deep cleft (Fig. 10A). Reid (1980) reported a large spherical mucus gland in the foot of *S. reidi*, but this was not located in our thin sections.

CTENIDIA

The ctenidia are large, brown, bipectinate and occupy most of the posterior half of mantle cavity (Fig. 12A, B). They are composed of around 170–180 crescentic lamellae about 20 μm in width. The distal edge of each leaflet is ciliated (Figs 13A, B, D), with a central tract of frontal cilia, bounded on each side by eulatero-frontal cirri made up of 10 pairs of cilia in two parallel rows (Fig. 13C). A broad band (ca 75 μm wide) of lateral cilia occupies the outer part of the lateral face of each lamella. The rest of each lamella is an unciliated, smooth, microvillii-covered surface. Along the proximal edge of the lamellae are a series of small projections bearing shaving-brush-like ciliary tufts set on short projections (ciliated knobs of Yonge, 1939) about 15 μm in diameter (Fig. 13F). Internally, the ctenidial lamellae comprise the distal ciliated section (120 μm in length) supported by a tapering, double chitinous rod (ca 12 μm in width) (Fig. 13D). At, and proximal to the rod, the ctenidial epithelium changes from cilia-bearing cells (ciliated zone) to the bacteriocyte zone (Fig. 13E) that occupies most of the length of the lamellae. Within the bacteriocyte zone, the lamellae comprise thin sheets of cells (8–10 μm wide) separated by central blood space (Fig. 14D). The epithelial cells are packed with elongate, rod-shaped bacteria (ca 6–7 μm in length, and 1 μm in width) oriented with their long axes normal to the lamellar surface and occupying most of the cell space (Figs 14B, C, E). Surface views of the lamellae (Fig. 14A) show the bacteriocytes to be around 10–20 μm in diameter.

By comparison, the ctenidial lamellae of *S. (Solemyarina) terraereginae* from Lizard Island are thinner (5–7 μm compared with 8–10 μm) and less tightly packed together than *S. (S.) velesiana*. The bacteriocytes (Figs 15) contain smaller, shorter bacteria (2–5 μm long compared with 6–7 μm) that are less densely packed and

vary in shape (pleomorphic) from narrow to subspherical (Fig. 15 B-D). A similar morphology for the bacteriocytes of *S. (S.) terraereginae* was recorded from TEM observations by Kreuger & Cavanaugh (1997).

PALPS AND ALIMENTARY TRACT

On either side of the foot are structures that have been interpreted as homologous with, although much shorter than, the palp proboscides of Nuculoidea (Waller, 1998). These are twisted, flap-like structures with cupped distal terminations that lie laterally across the foot with, proximately, a ciliated groove leading to the mouth (Fig 12, E, G). All surfaces of the distal portions of these flaps are covered in ciliary tufts (Fig 12F). We did not observe any structure on the foot similar to the pouch-shaped, ciliated organ described by Reid, 1980 for *S. reidi*.

The mouth is small, with a narrow oesophagus leading to the very small stomach, with the digestive diverticula comprising just few short acini (Fig. 11B). The mid gut is thin and straight, leading to a narrow rectum that passes through the ventricle (Fig. 15), then dorsally to the posterior adductor and terminates at the posterior mantle aperture.

HYPOBRANCHIAL GLAND.

A hypobranchial gland occupies the posterior end of mantle cavity covering the outer surface of the visceral mass and extending ventrally to cover both dorsal and ventral surfaces of the ctenidial axes (Fig. 15A). Dorsal extensions of the glands line the dorsal inner mantle (Fig. 15B). A similar, extensive, hypobranchial gland has been recorded in *Solemya togata* (Pelseneer 1891; Stempell 1899) and *S. parkinsonii* (Morton 1977). In section, the gland comprises large mucous cells separated by narrow, ciliated cells similar to those described for *Solemya parkinsonii* (Morton 1977).

DISCUSSION

Previously, only three species of Solemyidae have been recorded from around Australia, the most well known being the large, southern species *S. australis*. Our recognition of four solemyids from Queensland and other putative species from limited sampling in South and Western Australia suggests that the diversity of

the family in Australia is underestimated, with small species having being largely ignored. Furthermore, amongst the described species there has been considerable nomenclatural confusion both at specific and supraspecific levels (e.g. Lamprell & Healy 1998). One of the problems in solemyid systematics is that shell characters are enigmatic and difficult to assess, for they lack features such shell sculpture and hinge teeth and are all uniformly covered by a distinctive, thick, shiny periostracum. Un-raveling of solemyid systematics would be a suitable case for molecular analysis but there are few available sequences from elsewhere lodged in GenBank and our sampling from Australia is very limited. Preliminary molec-ular results, combined with observations on morphological characters of the ligament and chondrophore and form of the posterior aperture and arrangement of surrounding papillae, support our discrimination of species. Further sampling around Australia is needed to establish the geographic ranges of the species and also to provide additional material for full formal descriptions of the unnamed small species from South and Western Australia. In the process of trying to place the Eastern Australia solemyids into a broader context we undertook a review of ligament and apertural characters of the type species of the recognised genera of Solemyidae, having realised that these are also often misunderstood and applied incorrectly. A particular example is the frequent use of the ligament characters of *Solemya* (*Austrosolemya*) *australis* as the type species of *Solemya* instead of, correctly, *Solemya togata*. Elaborating from Dall (1908a, b), characters of the ligament suggest a number of distinct groups of solemyids that can be tested as more molecular data becomes available.

Of the bivalve families possessing symbiosis with sulphide-oxidising bacteria, the Solemy-idae and Lucinidae are the only ones with species commonly inhabiting intertidal and shallow waters, where they live within the sediment at the boundary between oxidised and anoxic zones (Stewart *et al.* 2005; Stewart & Cavanaugh 2006). In both families, the symbiosis seems to be obligate, with some solemyids dependent to the point where the gut is entirely lost.

Morphological evidence from fossils suggests that the symbiosis is ancient in solemyids (Pojeta 1988; Cope 1996a), with the unusual features of the family, compared with the Nuculidae sister group, resulting from a long co-evolutionary history with symbiotic bacteria. Studies on *Solemya velum* and *S. reidi* show that the bivalves live in U and Y shaped mucus-lined burrows with a vertical tube reaching deeply into the anoxic zone (Stanley 1970; Reid 1980). By contrast with Lucinidae, the solemyids are more dynamic in behaviour, actively moving up and down within the burrows between the oxidised and sulphide-rich, anoxic sediment zones. The cylindrical shape, flexible shell, thick shiny periostracum and prehensile, digitate foot coupled with swim-ming ability may be considered as adaptations to this unusual and ancient lifestyle.

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Two new *Agaue* species (Acari: Halacaridae) from Moreton Bay, Queensland, with a key to Australian species

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ABSTRACT

Two new species, *Agaue fuscata* and *A. lubrica*, are described. *Agaue fuscata* is characterised by its conspicuously brown cerotegument, the four dorsal setae on PE and short legs. *Agaue lubrica* is rather slender, its integument is almost smooth and the cerotegumental cover delicate; the PE bears three dorsal setae. A key to the Australian *Agaue* species is given. ❑ *Australia, Queensland, marine mites, descriptions, new species, key*

More than a century ago, Lohmann (1889) introduced *Agaue* to include the single type species, *Agaue parva* (Chilton, 1883). Other species were subsequently added. Viets (1927), when surveying and reorganising the halacarid genera, redescribed the type of *Agaue parva* and the characters of *Agaue*, and erected *Aganopsis* for the species that had been erroneously placed into *Agaue*. These two genera, together with the majority of the other halacarid genera, were included in the just erected subfamily Halacarinae Viets, 1927.

Agaue proved to share numerous characters with *Halixodes* Brucker & Trouessart, 1900 and *Bradyagaue* Newell, 1971. Bartsch (1983) moved *Agaue* and *Bradyagaue* to the subfamily Halixodinae Viets, 1927, because of characters such as: the idiosoma and legs often bearing cerotegumental lamellae; a parallel-sided, slender gnathosoma with its two pairs of maxillary setae inserted adjacently near the basis of rostrum; a long rostrum with pair(s) of barbs at its apex; the seta on P-3 in dorsal position; the chelicerae slender and bearing large tines at their claws; the legs slender and their tibiae with smooth ventral setae, none of the setae pectinate or spiniform; the solenidion on tarsus I in dorsolateral, on tarsus II in dorsomedial position; the generally large fossa membranes on the tarsi; the large paired claws. The Halixodinae had previously included

only the two genera *Halixodes* and *Parhalixodes* Laubier, 1960 (Laubier 1960).

However the descriptions of many new halacarid species has increased the knowledge of intrageneric variations, and the range of character states has proved to be larger than expected. Characters thought to be unique to *Agaue* and other halixodines (e.g. the cerotegumental membranes) were also found in genera of other subfamilies. As there was no longer a unique combination of synapomorphies to justify a subfamilial separation of these four genera, the subfamily Halixodinae was abandoned and *Agaue* was returned to the Halacarinae (Bartsch 1998). Even so, the Halacarinae is not a natural unit, but includes genera with a variety of characters, and is in need of a reorganisation.

Three species of *Agaue* were present in samples taken at the low water mark around North Stradbroke Island, Queensland, two species in samples from Amity Point, *Agaue galatea* Otto, 1999 and *A. lubrica* sp. nov., and one species from Point Lookout, *Agaue fuscata* sp. nov.

MATERIAL AND METHODS

The specimens described were collected from the northern end of North Stradbroke Island, in Moreton Bay, a large sheltered embayment adjacent to Brisbane and south of the tropical

Great Barrier Reef (see Davie 2004, for general overview). Various substrata, algae, colonial organisms, sediment, were sampled from the upper tidal to just beneath the low water edge. The samples were washed with a jet of water over a 100 μm sieve. The material retained in the sieve was scanned for halacarid mites. The mites were cleared in lactic acid and mounted in glycerine jelly. The illustrations were prepared with help of a drawing tube. The holotypes and a voucher specimen are deposited in the Queensland Museum, Brisbane (QM).

Abbreviations used in the descriptions: AD, anterior dorsal plate; ads, adanal setae; AE, anterior epimeral plate; ds-1 to ds-5, first to fifth pair of dorsal idiosomal setae, numbered from anterior to posterior; GA, genitoanal plate; GF, genital foramen; GO, genital opening; OC, ocular plate(s); P-2 to P-4, second to fourth palpal segment; pas, parambulacral seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate(s); pgs, perigenital setae. The legs are numbered I to IV. The position of a seta or gland pore is given in a decimal system, with reference to the length of a plate, from its anterior to posterior margin.

SYSTEMATICS

Agaue Lohmann, 1889

Type Species: *Halacarus parvus* Chilton, 1883.

Diagnosis. *Idiosoma.* With cerotegument, generally forming membranes or lamellae. One pair of gland pores each on or lateral to AD, on OC and PD. PE with one to three dorsal setae anterior to leg III, and zero to one setae anterior to leg IV. Female GA with 3–15 (rarely more) pairs of pgs. Male GA with more than 80 pgs densely arranged around GO; genital sclerites with five pairs of spur-like sgs.

Gnathosoma. Generally slender. Tectum with scaliform lamella. Rostrum almost parallel-sided. Maxillary setae inserted close together. Rostral setae minute, one pair spur-like or divaricate. Palps four-segmented. P-3 short, usually with one distodorsal bristle; that seta slender or flattened. P-4 with three setae in basal whorl (rarely situated in apical half of segment), one seta in about middle of segment, and one setula and two spurs at its tip. Chelicerae slender, cheliceral claw with few but strong teeth.

Legs. Often with cerotegumental lamellae. Genua shorter than telofemora and tibiae. Tibiae cylindrical or clavate, with four to six smooth ventral setae. Tarsi with large membranes of claw fossae. Tarsus I with one ventromedial seta, tarsi II to IV without such setae. Tip of tarsus I with cluster of 10–30 ventral eupathidia. Paired claws large, median claw minute.

Agaue fuscata sp. nov.
(Figs 1, 2)

Material Examined. HOLOTYPE, QM-S83653, ♀, Frenchmans Beach, Point Lookout, North Stradbroke I., Queensland (c. 27°26'S, 153°33'E), *Halimeda* sp. (Chlorophyta), in tidal rock pool, 23.02.2005, I. Bartsch.

Diagnosis. Length of idiosoma 485 μm. Dorsal plates with delimited cerotegumental costae, these costae of brown colour. AD wider than PD. Corneae small. PE with three dorsal setae anterior to insertion of leg III and one seta anterior to leg IV. Female GA with 16 small pgs around GO. Ovipositor extending beyond GA. Gnathosoma 0.34 times of length of idiosoma, 1.7 times longer than wide. Length of rostrum 2.3 times that of gnathosomal base. Legs short, length of telofemora II and III about twice their height. Tibiae not markedly club-shaped. Tibiae I to IV with four ventral setae each. Claws with tines on accessory process and shaft.

Description. *Female.* Idiosomal length 485 μm, width 309 μm. Cerotegumental costae of dorsal plates rather smooth, of brown colour, without sculpturing. Plates with areolae with numerous deep pores, else surface of dorsal plates smooth. Length of AD (without anterior lamella) 155 μm, width 164 μm, plate widest at the level of gland pores. AD with pair of longitudinal cerotegumental costae, about 50 μm in width, and a transverse anterior cerotegumental area (Fig. 1A). Integument along lateral margin of AD with deep pores. Markings from muscle attachment small and in posterior half of plate. Length of OC 97 μm, width 75 μm. Plate with two very small corneae; lateral margin with pore canaliculus followed by gland pore. Integument with deep pores both along lateral and medial margin. Length of PD 264 μm, width 157 μm; pair of cerotegumental costae about 45 μm wide; with numerous deep pores on either side of cerotegumental costae. Pair of gland pores at 0.9 relative to
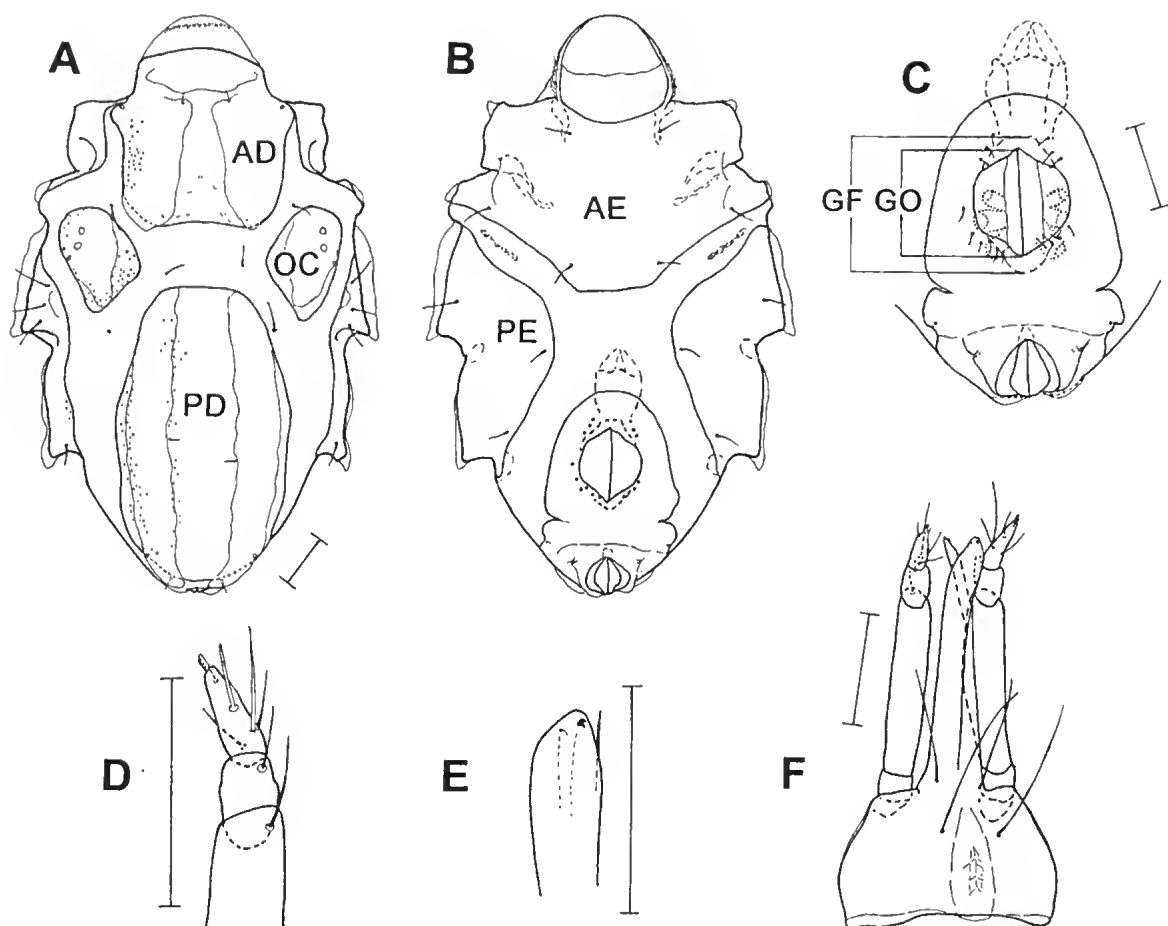
FIG. 1. *Agaue fuscata* sp. nov., holotype ♀: **A**, Idiosoma, dorsal (margin of plates in finely broken line when obscured by cerotegument); **B**, idiosoma, ventral; **C**, genitoanal plate and ovipositor; **D**, end of palp, dorsolateral; **E**, tip of right half of rostrum, ventral; **F**, gnathosoma, ventral. (AD = anterior dorsal plate; AE = anterior epimeral plate; GF = genital foramen; GO = genital opening; OC = ocular plate; PD = posterior dorsal plate; PE = posterior epimeral plate) Scale bar = 50 μm.

length of PD. All dorsal setae small, without cerotegumental cover. Pair of ds-1 smaller than following setae and inserted in anterior margin of pair of cerotegumental costae. Pairs of ds-2, ds-3 and ds-4 within striated integument; ds-5 on PD. Pair of ads on anal plate, obscured by cerotegument of PD.

Surface of ventral parts of plates with delicate, minutely reticulate and filamentous cerotegumental cover, margins of ventral plates with thick, smooth cerotegument. Ventral setae short, slender. Length of AE 150 μm, width 282 μm; its posterior margin truncate (Fig. 1B). Plate with three pairs of setae. Epimeral processes lamellar, with numer-

ous filaments. Length of PE 235 μm; with seven setae, namely three dorsal setae anterior to insertion of leg III, one dorsal seta anterior to leg IV and three ventral setae. Length of GA 180 μm, width 120 μm; anterior margin rounded. GF constricted by thin lamellae. Length of GO 65 μm, width 55 μm. With 16 very short pgs around GO; no setae in or near anterior margin of GA (Fig. 1C). Interval between anterior margin of GA and GO 0.5 times length of GO, distance from GO to end of anal sclerites 1.3 times the length of GO. Ovipositor extending beyond margin of GA.

Length of gnathosoma 167 μm, i.e. 0.34 of idiosomal length; width 97 μm. Rostrum about 2.3
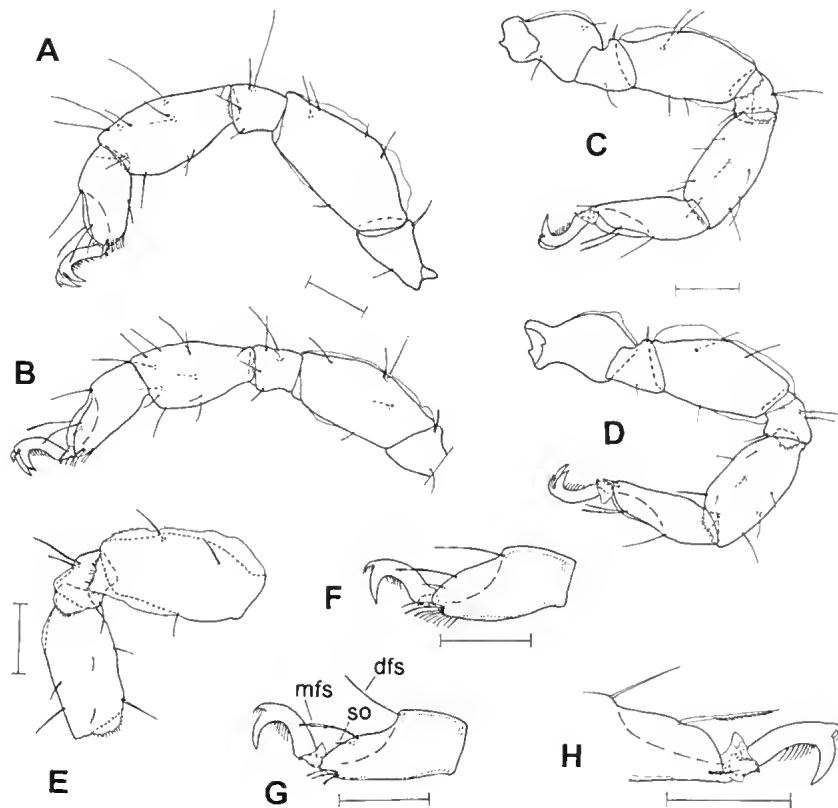
FIG. 2. *Agaue fuscata* sp. nov., holotype ♀: **A**, Basifemur to tarsus I, medial; **B**, basifemur to tarsus II, medial; **C**, leg III, medial; **D**, leg IV, medial; **E**, telofemur, genu and tibia IV, lateral (outline of segments in broken line when obscured by cerotegument); **F**, tarsus I, lateral (medial setae and claw omitted) (dotted lines indicate thickness of integument); **G**, tarsus II, medial (lateral fossary seta, parambulacral setae and claw omitted); **H**, tip of tarsus IV, medial (lateral fossary and parambulacral seta omitted). (dfs = dorsal fossary seta; mfs = dorsomedial fossary seta; so = solenidion) Scale bar = 50μm.

times longer than gnathosomal base. Tectum scaliform, arched. Basal pair of maxillary setae slightly longer than following pair of setae (Fig. 1F). Rostral sulcus extending almost to base of rostrum. Tip of rostrum with pair of minute bidentate spurs and delicate setulae (Fig. 1E). Dorsal setae on P-2 and P-3 slender, smooth, more slender than dorsal seta of basal whorl of P-4 (Fig. 1D). P-4 with three basal setae, an eupathid lateral seta in middle of segment and a wide setula and two spurs apically.

Legs short, wide. Length/height ratio of telofemora I to IV: 2.3, 2.1, 2.0, 2.0. All telofemora longer than tibiae (Fig. 2A–D). Telofemora with cerotegumental cover, i.e. two dorsal cerotegumental ridges which extend along medial and

lateral flank to ventral flank. Dorsal ridges slightly thicker than ventral cerotegument, and thicker on telofemora III and IV than on telofemur II. Telofemora, genua and tibiae with thin articular lamellae of cerotegument; lamellae along their distal margin with delicate filaments (Fig. 2E). Tarsi with large fossa membranes. Leg chaetotaxy (solenidia and pas included): leg I, 1, 2, 5, 4, 11, 24; leg II, 1, 2, 5, 4, 11, 10; leg III, 2, 2, 3–4, 4, 9, 5; leg IV, 0, 2, 3, 3, 9, 5. Dorsal seta on basifemora III and IV wider than ventral seta. Ventromedial setae of tibiae remarkably short and delicate. Dorsomedial and -lateral fossary setae of tarsi slightly widened and plumulose. Tarsus I with one ventromedial seta in about middle of segment and cluster with 19 eupathidia at its apex

(pas included); solenidion on dorsolateral fossa membrane (Fig. 2F), its length 14 μm. Solenidion on tarsus II in medial fossa membrane (Fig. 2G), length 9 μm; apex of tarsus II with pair of eupathidia and doubled pas. Tarsi III and IV each with pair of short pas.

Paired claws large; central sclerite with minute dent-like process. Paired claws with large accessory process. Process with tines; shaft of claws with about eight large and some smaller tines (Fig. 2H).

Remarks. *Agaue fuscata* is characterised by its brown, smooth cerotegument on the idiosoma and legs, the four dorsal setae on the PE, three anterior to the insertion of leg III, one immediately anterior to that of leg IV, and the tarsi with coarse tines both on the accessory process and claw shaft. Eleven named species of *Agaue* had to date been recorded from Australian shores, namely, *A. aliena* Otto,1999, *A. bella* Otto, 1999, *A. brevipes* Bartsch, 1999, *A. circellaris* Bartsch 1999, *A. galatea* Otto, 1999, *A. hispida* (Lohmann, 1893), *A. reichelti* Otto, 1999, *A. scita* Bartsch, 1999, *A. similis* Bartsch, 2007, *A. subglabra* Bartsch, 1999, and *A. tenuipes* Bartsch, 1999. *A. brevipes* and *A. tenuipes* share the just mentioned characters but the cerotegument lacks the intense brown colour present in *A. fuscata* and their AD is more slender than their PD whereas in *A. fuscata* the AD is wider than the PD.

Posterior epimeral plates with four dorsal setae and claws with tines on the accessory process and the shaft are characters present also in *A. californica* (Hall, 1912), *A. setalis* Newell, 1984, and *A. variabilis* MacQuitty, 1984. *Agaue californica* and *A. variabilis* are species of the eastern Pacific, present from Mexico to Oregon, the former as far as to Washington (Hall 1912; MacQuitty 1984), records of *A. setalis* are from Western Antarctica (Newell, 1984). The cerotegument on the dorsal plates and the telofemora of *Agaue californica* and *A. variabilis* is not smooth, as in the Australian species, but panelled. The AD of *A. fuscata* is wide, the posterior half of the plate rectangular, whereas the opposing margins of AD and PD are ovate in *A. variabilis* and arched in *A. californica* and *A. setalis*. In that latter species the cerotegumental areolae of the AD are faint and converging.

Etymology. The specific name is derived from fuscatus (Latin), in reference to its dark colour.

Agaue lubrica sp. nov.
(Figs 3, 4)

Material Examined. HOLOTYPE, QM-S83654, ♀, Amity Point, North Stradbroke I., Qld (c. 27°25′S, 153°26′E), amongst corallines and other red algae growing on stones, low water edge, 20.02.2005, I. Bartsch.

Diagnosis. Length of idiosoma 560 μm. Dorsal plates very delicately punctate, without areolae with deep pores. Cerotegumental cover almost inconspicuous. Dorsal setae short. PE with three dorsal setae anterior to insertion of leg III, none anterior to leg IV. Female GA with 27 pgs, situated around GO and along anterior margin of GA. Gnathosoma long and slender, almost half length of idiosoma. Rostrum almost twice length of gnathosomal base. Tibiae slender, cylindrical. Tibiae I, III and IV with four ventral setae. Telofemora at least three times longer than high. Claws with accessory process, otherwise smooth.

Description. *Female.* Idiosomal length 560μm, width 320 μm. Cuticle of dorsal plates delicately punctate, at low magnification almost smooth; areolae with scattered deep pores lacking; cerotegumental cover delicate. Integument between plates finely striated. Length of AD 165 μm, width 184 μm; anterior margin truncate, with delicate lamella; posterior margin arched. Markings of internal muscle scars distinct, arranged in shape of a triangle. Pair of gland pores in lateral margin of AD on tiny cones (Fig. 3A). Length of OC 100 μm, width 65 μm; slightly raised corneal area with two small corneae, eye pigment beneath corneae, and a gland pore on small cone posterior to cornea. Interval between gland pore and cornea twice the latter's diameter. Pore canaliculus immediately lateral to posterior cornea, anterior to gland pore. Length of PD 300 μm, width 184 μm; anterior margin truncate. With pair of very faint cerotegumental costae; integument beneath cerotegument delicately punctate. Pair of gland pores at 0.9. All dorsal setae small, without conspicuous cerotegumental cover. Pair of ds-1 on AD, slightly anterior to level of gland pores. Pairs of ds-2 to ds-4 within striated integument. Pair of ds-5 minute, at 0.5 relative to length of PD, that equals level with insertion of leg IV. Pair of ads in margin of anal plate.

Ventral plates delicately dotted. Length of AE 175 μm, width 284 μm; with three pairs of setae. Length of PE 224 μm; with three ventral and
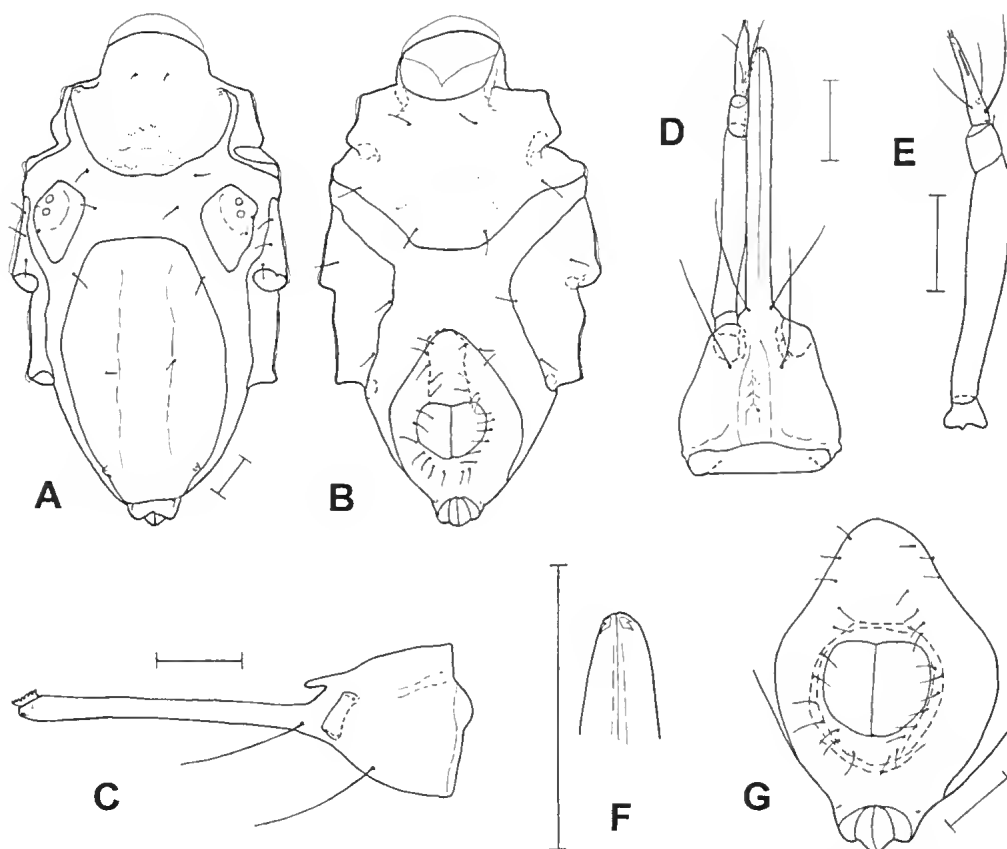
FIG. 3. *Agaue lubrica* sp. nov., holotype ♀: **A**, Idiosoma, dorsal; **B**, idiosoma, ventral; **C**, gnathosoma, lateral; **D**, gnathosoma, ventral; **E**, palp, lateral; **F**, tip of rostrum, ventral; **G**, genitoanal plate. Scale bar = 50μm.

three dorsal (marginal) setae, the latter anterior to insertion of leg III; no dorsal seta anterior to insertion of leg IV. PE hardly extending beyond insertion of leg IV. Length of GA 222μm, width 150 μm; anterior margin ovate (Fig. 3B). Length of GF 90 μm, width 80 μm, constricted by lamellae, accordingly GO smaller than GF, length 60 μm, width 72 μm. GO almost in middle of GA (Fig. 3G); distance from GO to anterior margin of GA equalling 1.3 times length of GO; distance from posterior margin of GO to end of anal cone 1.2 times length of GO. In all, 12 and 15 pgs in either half of GA or immediately outside the plate; 8 and 11 of pgs situated close to GO. Subgenital setae lacking. Ovipositor reaching till end of GA.

Length of gnathosoma 264 μm, width 100 μm, i.e. almost half of idiosomal length. Integument of gnathosomal base delicately punctate. Rostrum slender, length 177 μm, almost twice length of gnathosomal base. Two pairs of maxillary setae almost equal in length (Fig. 3C); distal pair of setae separated from basal pair by more than distance between that latter pair (Fig. 3D). Tectum scaliform. One pair of rostral setae, at tip of rostrum, in form of divaricate spurs (Fig. 3F), the other pair small, delicate and in lateral margin of rostrum. P-2 with slender dorsal seta; P-3 with slender, short dorsal seta (Fig. 3E). Length of P-4 about three times that of P-3; three setae in basal third of segment; one lateral eupathid seta in about middle of P-4; apically with two spurs and one setula.

Segments of legs cylindrical, tibiae not clavate (Fig. 4A–D). Telofemora I and II longer than tibiae. Telofemora I to IV about 3.5, 3.3, 3.4, 3.1 times longer than high, respectively. Telofemora
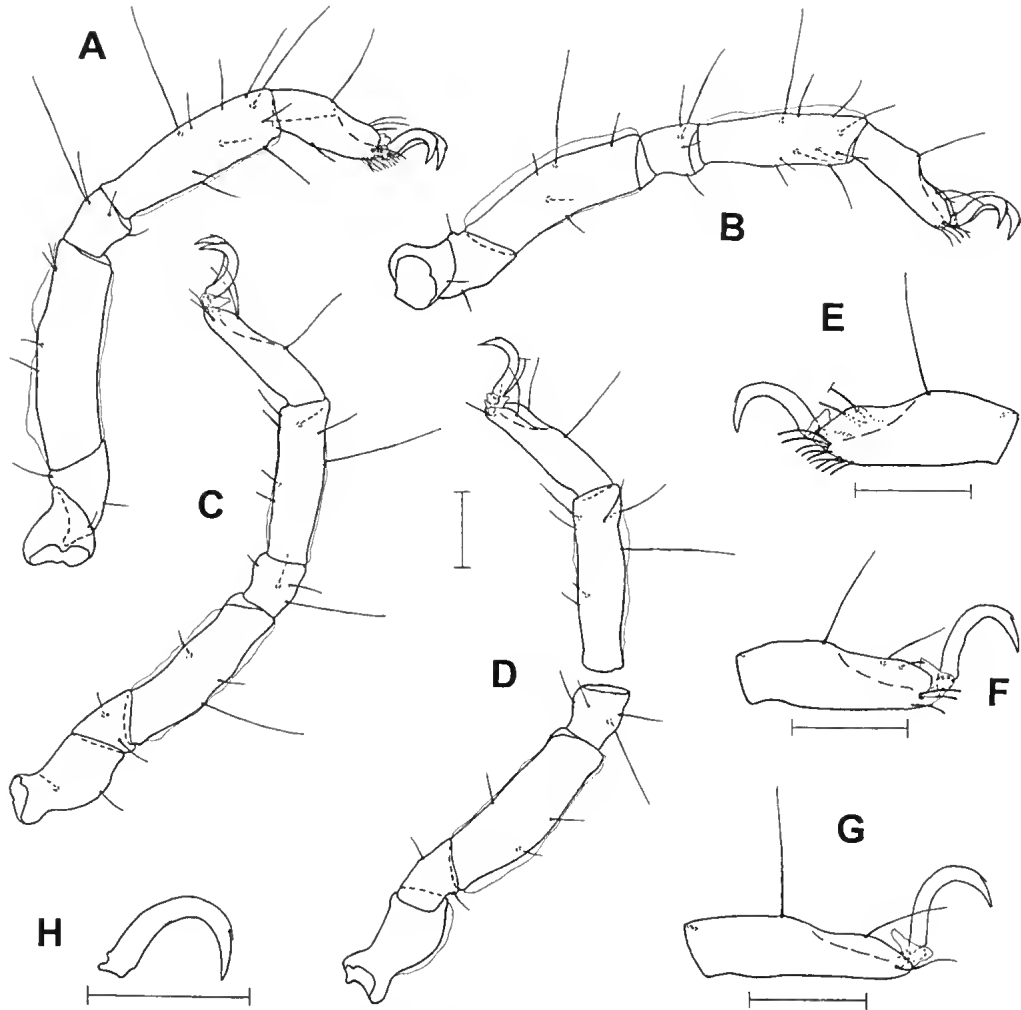
FIG. 4. *Agaue lubrica* sp. nov., holotype ♀: A, Leg I, medial; B, leg II, medial; C, leg III, medial; D, leg IV, medial; E, tarsus I, lateral (medial setae and claw omitted); F, tarsus II, medial (lateral fossary seta, parambulacral setae and claw omitted); G, tarsus III, lateral (medial setae and claw omitted); H, claw II, inner flank. (A–D, telofemora and tibiae with cover of debris instead of distinct cerotegumental lamellae) Scale bar = 50 μm.

with cover of debris (Fig. 4A–D); distinct cerotegumental ridges or lamella lacking. All tarsi with large fossa membranes. Leg chaetotaxy (solenidia and pas included): leg I, 1, 2, 4, 4, 11, 19; leg II, 1, 2, 5, 4, 10, 10; leg III, 2, 2, 3, 4, 7, 5; leg III, 0, 2, 3, 4, 7, 5. No ventral seta on telofemur I; telofemora II to IV with one ventral seta each. Each of tibiae I, III and IV with four ventral setae; tibia II with two ventral, two ventrolateral and two ventromedial setae. Tarsi I to IV with three long dorsal setae, of these the two apical setae paired, inserted on fossa membranes. Solenidion

on tarsus I 12 μm long, on dorsolateral fossa membrane (Fig. 4E). Solenidion on tarsus II on dorsomedial fossa membrane (Fig. 4F), its length 9 μm. Tarsus I with one ventromedial seta and an apical cluster with 14 eupathid setulae, pas included. Tarsi II to IV without ventral setae. Apex of tarsus II with pair of eupathidia and doubled pas, six setae in all. Tarsi III (Fig. 4G) and IV each with pair of tapering pas.

Claws of all tarsi with accessory process; shaft of claws apparently smooth though, at high magnification, about five delicate tines seen on
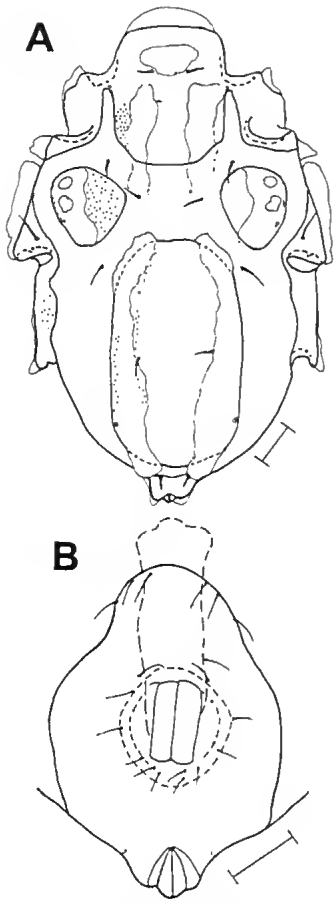
FIG. 5. *Agaue galatea* Otto, 1999, ♀: **A**, Idiosoma, dorsal (margin of PD in finely broken line when obscured by cerotegument); **B**, genitoanal plate and ovipositor. Scale bar = 50 μm.

inner flank of claws II to IV (Fig. 4H). Central sclerite without claw-like process.

Remarks. *Agaue lubrica* has slender legs with cylindrical tibiae and there are three dorsal setae on the PE anterior to the insertion of leg III. The same combination of characters is found in *A. brevipes*, *A. circellaris*, *A. fuscata*, *A. similis*, *A. subglabra*, and *A. tenuipes*. The other *Agaue* species known from Australia have a single dorsal seta on the PE and the tibiae are club-shaped. The six species just mentioned have distinct cerotegumental costae whereas in *A. lubrica* the cerotegument is faint. Females of *A. brevipes*, *A. fuscata*, *A. similis*, and *A. tenuipes* have the GO in the anterior half of the GA, but in *A. lubrica* the GO is in the middle of the GA. In *A. subglabra*

the ds-3 stand close together relative to their distance to the OC, there are no setae in the anterior part of the female GA and the ovipositor extends distinctly beyond the level of the anterior margin of the GA; in *A. lubrica* the interval between the pair of ds-3 is larger than that between the ds-3 and the margin of the OC, in the female there are several setae near the anterior margin of the GA, and the ovipositor extends to, but not beyond, the anterior margin of the GA. *A. circellaris* is much larger than *A. lubrica*, has prominent cerotegumental lamellae, a very slender gnathosoma, and six ventral setae on tibiae I, III and IV.

Other superficially similar species are *A. insignata* Bartsch, 1979, *A. longiseta* Newell, 1951, *A. magellanica* Newell, 1951, *A. marginata* Viets, 1950, *A. setalis* Newell, 1984, and *A. variabilis* MacQuitty, 1984, but in all these species the cerotegumental lamellae and the ornamentation of the plates are more conspicuous than in *A. lubrica*. Worldwide, 44 *Agaue* species are known (Bartsch 2004, 2007, present new records; Chang & Chatterjee 2006).

Etymology. The specific name is derived from lubricus (Latin), smooth or slippery, referring to its almost smooth integument.

Agaue galatea Otto, 1999
(Fig. 5A, B)

Agaue galatea Otto, 1999: 276–278, figs 5A–D, 6A–D.

Material Examined. QM-S83655, ♀, Amity Point, North Stradbroke I., Qld (c. 27°25'S, 153°26'E), amongst small hydrozoans and bryzoans on stones, mid-tide, 12.02.2005, I. Bartsch.

Diagnosis. Length of idiosoma 545 μm. Idiosoma and legs with smooth cerotegument; AD with unpaired transverse and pair of parallel-sided longitudinal lamellae. Plates with areolae with canaliculi. Dorsal idiosomal setae with cerotegument. PE with single dorsal seta. Female GA with 19 pgs. Ovipositor extending beyond GA. Length of gnathosoma 2.2 times its width and length of rostrum about twice that of gnathosomal base. Integument of gnathosomal base with coarse porosity. Basal pair of maxillary setae longer than following pair. Tibiae clavate. Telofemora 2.7–3.1 times longer than high. Leg chaetotaxy, from trochanter to tarsus (solenidia and pas included): leg I, 1, 2, 5, 5, 12, 22; leg II, 1,

2, 5, 5, 9–10, 11; leg III, 2, 2, 3, 3, 8, 5; leg IV, 0, 2, 3, 3, 7, 5. Tibiae I to IV with 6, 4, 4, 4 ventral setae. Claws with accessory process and five to six tines at the claw shaft.

Supplementary Description. *Female.* Idiosomal length 542 μm. AD with transverse and pair of longitudinal cerotegumental areas; PD with pair of costae extending slightly beyond anterior margin of PD. Plates with areolae with deep pores (Fig. 5A). On AD deep pores along postero-lateral portion of plate, on OC scattered deep pores along lateral margin but numerous in medial part, medial to cerotegumental cover, on PD two narrow lines with deep pores on either side of cerotegumental costae. PE with deep pores between insertions of legs III and IV, close to dot with cerotegument. Striated integument with delicate cerotegumental cover. Pore canaliculus in lateral margin of OC at the level of posterior cornea but more or less obscured by pores. Posterior cornea not distinctly delimited, interval between cornea and gland pore equalling about diameter of cornea. Pair of ds-5 on PD at 0.5. In female GO in middle of plate (Fig. 5B), distance to anterior margin of GA equalling 1.4 times length of GO, distance to tip of anal sclerites 1.7 times. GA with 19 pgs.

Length of gnathosoma 195μm, width 90μm, i.e. 2.2 times longer than wide and 0.36 of idiosomal length. Length of rostrum 130 μm or twice that of gnathosomal base. Basal pair of maxillary setae at least three times length of following pair. Rostral sulcus extending to that pair of maxillary setae.

Telofemora I and II longer than these legs tibiae, telofemora III and IV shorter than tibiae. Length/height ratio of telofemur I 3.1, that of telofemora II to IV 2.7–2.8. Dorsal cerotegumental cover of telofemora less than 1/3 of height of segment. Claws with accessory process and five to six tines at the claw shaft.

Remarks. When sorting at low magnification, *Agaue galatea* is similar to *A. fuscata* and *A. lubrica*, but its cerotegumental cover is pale, not as dense and brown as in *A. fuscata*, and more conspicuous than in *A. lubrica*. Other differences include: *A. galatea* has a single dorsal seta on the PE anterior to the insertion of leg III, while in *A. fuscata* and *A. lubrica* there are three dorsal setae anterior to leg III; the tibiae I of *A.*

galatea bear six ventral setae, but the tibiae I of *A. fuscata* and *A. lubrica* have four ventral setae; the dorsal plates of *A. galatea* and *A. fuscata* have areolae in which the integument is pierced by deep pores, but such areolae are lacking in *A. lubrica*.

In the specimen described by Otto (1999: fig. 5A) the ds-5 are situated at 0.7 instead of at 0.5 as in the specimen from North Stradbroke I., and the length of the rostrum is 1.4 times that of the gnathosomal base, instead of twice the gnathosomal base.

AGAUE IN AUSTRALIA

The first records of species of *Agaue* from Australia were published about a century ago (Lohmann 1893, 1909), and included a deutonymph of *A. hispida*, from off Sydney, and species similar to *A. chevreuxi* (Trouessart, 1889) and *A. panopae* (Lohmann, 1893) with records from Sydney and Shark Bay. Twelve species have since been described from Australia, six species from the southwestern coast (*A. brevipes*, *A. circellaris*, *A. tenuipes*, *A. scita*, *A. similis*, and *A. subglabra*) (Bartsch 1999a, b, 2007), and six from the eastern coast (*A. aliena*, *A. bella*, *A. fuscata*, *A. galatea*, *A. lubrica* and *A. reichelti* (Otto 1999; above described new species).

Agaue hispida was described on the basis of a single deutonymph. Its length, with the gnathosoma included, is 430μm, which equals an idiosomal length of about 330μm. The dorsal plates are ornamented with a reticulate cerotegument, the legs bear large honey comb-shaped cerotegumental lamellae, and the width of the lamellae on telofemora and tibiae is at least half the height of the relevant segment. The walls of the honey comb are drawn out into numerous points. The ds-3 are very long. The Australian species *A. aliena*, *A. bella*, *A. reichelti*, and *A. scita* also have large honey comb-shaped lamellae but the cerotegument does not show a reticulate pattern. Deutonymphs in general have less developed cerotegumental ornamentation and smaller lamellae than their adults, but the situation in adults cannot definitely be predicted on the basis of nymphal characters.

The identity of the Australian species recorded under the names *A. panopae* and *A. chevreuxi*

(Trouessart, 1889) is unknown. Material of *A. panopae* from off Sydney was mentioned in the original description (Lohmann 1893: 72), but the specimen illustrated and the first mentioned locality is from off the Cape Verde Islands and, accordingly, that specimen and locality should be regarded as the type and type locality of *A. panopae*. According to present knowledge of distribution, one may expect different species of *Agaue* to occur in the Atlantic and Pacific Oceans. Lohmann (1893: pl. 4, fig. 9) presented a ventral aspect of a female from off Sydney, that Australian specimen may be closely related or conspecific with *A. galatea*; though the given length of the idiosoma (350–420μm) and the dorsal aspect of the gnathosoma (pl. 3, fig. 8), with a short, wide seta on P-3, do not agree with the characters found in *A. galatea*. The type locality of *A. chevreuxi* is Le Croisic at the French Atlantic coast (Trouessart 1889). Both *A. chevreuxi* and *A. panopae* are wide-spread in the warm-temperate Atlantic and the Mediterranean (Lohmann 1893; Viets 1940; Mari & Morselli 1990), the former also in the Black Sea (Bartsch 1998).

The following key includes the twelve *Agaue* species definitely known from Australia, *A. aliena*, *A. bella*, *A. brevipes*, *A. circellaris*, *A. fuscata*, *A. galatea*, *A lubrica*, *A. reichelti*, *A. scita*, *A. similis*, *A. subglabra*, and *A. tenuipes*, but excludes *A. hispida* which is known only by its deutonymph.

Key to Adults of Australian Species of *Agaue*

1. Rostrum more than three times length of gnathosomal base. P-4 with whorl of setae in distal quarter. . . . . *A. circellaris*
— Rostrum less than 2.5 times length of gnathosomal base. P-4 with whorl of setae in basal two-thirds. 2

2. Rostrum and palps short, not longer than gnathosomal base. First pair of gland pores and dorsal setae on dorsal portion of AE. . . . . *A. scita*
— Rostrum and palps long and slender, more than 1.5 times length of gnathosomal base. First pair of gland pores and dorsal setae on AD. 3

3. PE with three or four dorsal setae, three setae anterior to insertion of leg III, zero or one seta anterior to leg IV. 4
— PE with single dorsal seta anterior to insertion of leg III. 9

4. Claws with J-shaped pecten with numerous tines along the claw shaft. PE with dorsal seta anterior to insertion of leg IV. In females distance between anterior margin of GA and GO less than length of GO . . . 5
— Claws with zero to six small tines in middle of claw shaft. PE without dorsal seta anterior to insertion of leg IV. In females distance between anterior margin of GA and GO equalling at least length of GO. 8

5. Telofemora slender, length of telofemora III and IV at least 2.7 times their height. . . . 6
— Telofemora III and IV less than 2.5 times their height. 7

6. Length of telofemora III and IV more than three times their height. . . . . . *A. tenuipes*
— Length of telofemora III and IV about 2.7–2.8 times their height. . . . . *A. similis*

7. AD wider than PD. Cerotegument of conspicuously brown colour. . . . . . *A. fuscata*
— PD wider than AD. Cerotegument pale. . . . . *A. brevipes*

8. Cerotegumental costae on AD in shape of inverted V. Pair of ds-3 situated close together, interval between setae same or less than their distance to margin of OC. Shaft of claws III and IV with four to six tines. . . . . *A. subglabra*.
— AD without such cerotegumental costae. Interval between setae ds-3 more than twice the distance to margin of OC. Shaft of claws III and IV apparently smooth. . . *A. lubrica*

9. Cerotegumental cover on idiosoma and legs plain, without conspicuous texture. . . . . *A. galatea*
— Cerotegumental cover on idiosoma and legs large and of filamentous texture. 10

10. Telofemora with large dorsal cerotegumental lamellae but inconspicuous ventral lamellae. Tibiae without lamellae. . . . . . . *A. aliena*
— Dorsal and ventral lamellae of telofemora large, almost equal in height. Tibiae with lamellae. 11

11. P-3 with dorsal seta. Corneae removed from margins of OC, their diameter less than 1/6 of length of OC. In females distance from anterior margin of genital foramen to that of GA almost twice length of foramen. . . . . *A. bella*
— P-3 without seta. Corneae close to margin of OC, their diameter about 1/3 of length of

OC. In females interval between anterior margin of genital foramen and that of GA somewhat more than length of foramen.   .
. . . . *A. reichelti*

ACKNOWLEDGEMENTS

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Halacarid mites (Acari: Halacaridae) in a freshwater influenced beach of North Stradbroke Island, Moreton Bay, Queensland

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ABSTRACT

Six species of halacarid mites were found in a sandy slope and an adjacent mud flat, both strongly influenced by freshwater. *Acarochelopodia biunguis* Bartsch, 1988, *Copidognathus psammobius* sp. nov. and *Halacaroides australiensis* sp. nov. are exclusively arenicolous, obviously tolerating freshwater saturation. *Copidognathus cooki* Bartsch, 2003, inhabits the mud flat; previous records are from brackish rivers and creeks. *Limnohalacarus billabongis* Bartsch, 1999, and *Lobohalacarus weberi* Romijn & Viets, 1924, are typically freshwater inhabitants. All species are diagnosed and the new species are described. ❑ *Australia, Halacaridae, marine littoral, brackish water, new species, description.*

The Halacaridae includes more than 1000 marine and about 50 freshwater species (Bartsch 1996, 2004). Several species belonging to marine genera can survive in brackish or even fresh water, while typically freshwater species are also regularly found in brackish water habitats. One of the beaches examined, with a small sandy slope and an adjacent mud flat, proved to be strongly influenced by freshwater, and samples from that beach contained a range of taxa that are normally variously classified as limnic, marine, or brackish. The interstitial fauna of the sediment from just above the freshwater table of the sandy slope contained, amongst others, the three species *Acarochelopodia biunguis* Bartsch, 1988, *Copidognathus psammobius* sp. nov. and *Halacaroides australiensis* sp. nov. The sediment at the lower edge of the slope and the adjacent flat was inhabited by the halacarid mites *Copidognathus psammobius, Copidognathus cooki* Bartsch, 2003, *Limnohalacarus billabongis* Bartsch, 1999 and *Lobohalacarus weberi* (Romijn & Viets 1924). The two latter genera are listed as freshwater, whereas *Acarochelopodia, Copidognathus* and *Halacaroides* are normally considered marine.

COLLECTION SITE

North Stradbroke Island is rich in a system of freshwater swamps and lakes paralleling the shore and freshwater often seeps into the adjacent Moreton Bay mudflats. Adam's Beach, south of the Dunwich ferry terminal, has such a seepage area. From the Moreton Bay landward there is a tidal muddy flat, with mangrove stands (*Avicennia*, Avicenniacea), small patches with *Juncus* (Juncaceae) and *Triglochin* (Juncaginaceae), a sandy beach slope, a small dune and behind that a freshwater swamp. The upper sediment layers in the tidal slope consisted of a medium coarse clean quartzite; in 10–30 cm depth, this sediment was replaced by a layer that included large amounts of phytal debris; the interstitial water became fresh. Freshwater was seeping into the flat along the lower edge of the slope, and during low tide, the salinity in the muddy surface layer was reduced to 2–3‰. A small subsurface freshwater creek, several centimetres in width and depth, extended for a few meters into the flat, easily recognisable because the sediment consisted of fine, oxygenated sand, in contrast to the adjacent flat with dense mud that turned anoxic

black immediately below the surface. The salinity in the subsurface sediment, in 3–5 cm depth, was 2–3‰ during low tide. During the high tide period, the flat and slope were covered by water of 30‰ and more.

MATERIALS AND METHODS

From the upper, middle and lower sandy slope, several sediment samples, 200–400 ccm each, were collected from just beneath the sediment surface to the groundwater horizon. From the lower edge of the slope and the tidal flat, amongst the *Triglochin* and *Juncus* stands, the surface layer of debris, less than 1 cm thick, was collected (sample volume less than 100 ccm). To get sediment from the subsurface freshwater creek a collecting jar, pressed into the sediment, was unlocked once it reached the subsurface position. All the samples were taken to the laboratory. The sediment samples were repeatedly stirred in water and the water decanted through a 100 μm net. Samples with debris were washed with a jet of water. The halacarids were extracted, using 12–25 x magnification, and preserved in ethanol. The mites were cleared in lactic acid and mounted in glycerine jelly. Holotypes and a number of paratypes and voucher specimens are deposited in the Queensland Museum, Brisbane (QM), other slides in the Senckenberg Museum, Frankfurt (SMF) and Zoological Institute and Zoological Museum, Hamburg (ZMH). Some voucher specimens have been retained in the author's collection (IBC).

Abbreviations used in the descriptions: AD, anterior dorsal plate; AE, anterior epimeral plate; ds-1 to ds-5, first to fifth (pair of) dorsal idiosomal seta(e), numbered from anterior to posterior; GA, genitoanal plate; GO, genital opening; GP, genital plate; OC, ocular plate(s); P-2 to P-4, second to fourth palpal segment; pas, parambulacral seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate(s); pgs, perigenital setae, numbered pgs-1, pgs-2, etc, from anterior to posterior. The legs are numbered I to IV. The position of a gland pore is given in a decimal system, with reference to the length of a plate, from its anterior to posterior margin. The diagnoses of the species are prepared on the basis of the Moreton Bay specimens.

RESULTS

The interstitial fauna of the sandy slope, just above the water table, was dominated by *Hexabathynella* sp. (Syncarida, Bathynellacea) and the three halacarid mite species *Acarochelopodia biunguis*, *Copidognathus psammobius* and *Halacaroides australiensis*. Other meiofaunal taxa were sparse, restricted to turbellarians, enchytraeids (Oligochaeta) and a few nematodes, harpacticoids and ostracods. The surface sediment of the bare flat and amongst the *Triglochin* stands held a rich meiofauna with tubellarians, nematodes, oligochaetes, harpacticoids, ostracods, and larvae of insects; the mite fauna was dominated by a species of the otherwise limnic oribatid genus *Trimaloconothrus* sp. (Acari: Malaconothridae), halacarids were represented by *Copidognathus psammobius* and *C. cooki*. The oxygenated sand of the subsurface creek held a rich mite fauna; most abundant was the oribatid *Trimaloconothrus* sp., followed by the halacarids *Limnohalacarus hillabongis* and *Lobohalacarus weberi*. Other taxa such as turbellarians, nematodes, oligochaetes and the larvae of insects, were rare, harpacticoids and ostracods lacking.

SYSTEMATICS

The genera are arranged in an alphabetical order, the diagnoses of the marine (*Acarochelopodia*, *Copidognathus*, *Halacaroides*) and freshwater genera (*Limnohalacarus*, *Lobohalacarus*) follow Bartsch (2006a, b).

Acarochelopodia Angelier, 1954
Type species: *Acarochelopodia delamarei* Angelier, 1954.

Acarochelopodia biunguis Bartsch, 1988
(Fig. 1A, B)

Acarochelopodia biunguis Bartsch, 1988: 217–218, figs 10–16; Otto, 2000: 125–126, figs 8a–i.

Material Examined. QM-S83656, ♂, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30'S, 153°24'E), upper slope, ground water table, 18.02.2005, I. Bartsch. IBC, ♂, deutonymph, data as above.

Diagnosis. Length of male 164–190 μm. All plates delicate, almost smooth. AD and PD subquadrangular. Pair of ds-1 on AD slightly posterior to level of gland pores. Pair of ds-5 on PD somewhat posterior to anterior margin of PD. Epimera I and II of either side fused, in the median divided; each plate posteriorly drawn out into
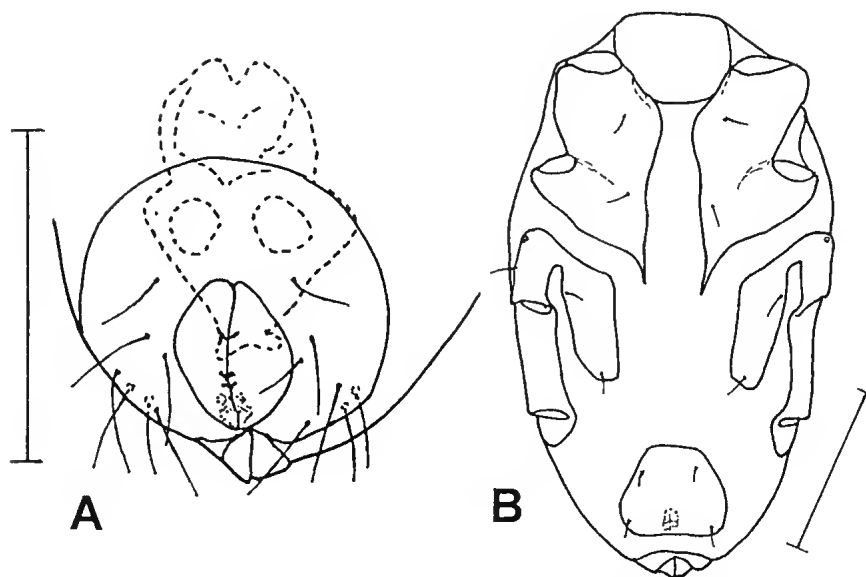
FIG. 1. *Acarochelopodia biunguis* Bartsch, 1988; **A**, Genitoanal plate, ♂; **B**, idiosoma, ventral, deutonymph. Scale line = 50 μm (A, QM-S83656; B, IBC).

narrow tail-like extension. Each of PE with longitudinal wedge, incompletely separating marginal from ventral portion; PE with gland pore, one dorsal seta and two ventral setae. Gnathosoma short, distal seta on P-2 much longer and wider than preceding seta. Leg chaetotaxy (pas excluded, solenidion included, large strongly denticulate spines in roman numerals): 1, 2, 3+I, 3+II, 3+VI, 7; leg II, 1, 2, 3, 4, 5, 5; leg III, 1, 1, 2, 3, 5, 4; leg IV, 1, 1, 2, 3, 5, 3. Spine of telofemur I short, in ventral position. Ventromedial spine of genu I short, ventrolateral one long. Tibia I with two and four long ventromedial and -lateral spines, respectively. Tarsus I slender, with one dorsal seta near base and two setae in about middle of segment. Tarsi II to IV with paired claws; central sclerite with minute tooth.

Supplementary Description. *Male*. GA with seven pairs of pgs (Fig. 1A). Genital sclerites with three pairs of short sgs. Internal genital acetabula in posterior GO. Spermatopositor extending beyond anterior margin of GA.

Deutonymph. Length of idiosoma 165 μm. Dorsal aspect similar to that of adults. Pair of AE posteriorly with tail-like, pointed extensions (Fig. 1B). PE incompletely divided and, as in adults, with gland pore, one dorsal seta and two ventral setae. GP quadrangular; with two pairs of pgs and two pairs of internal acetabula.

Distribution & Biology. First recorded from Hawaii (Bartsch 1988), with a second record from Queensland, from just north of Cairns (Otto 2000). All records are from tidal beaches. The recent record from North Stradbroke I. is the only one from almost freshwater. The species is expected to be spread in the tropical and warm-temperate Pacific Ocean.

Copidognathus Trouessart, 1888

Type species: *Copidognathus glyptoderma* Trouessart, 1888.

Copidognathus psammobius sp. nov.
(Figs 2A–F, 3A–H)

Material Examined. HOLOTYPE: QM-S83657, ♂, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30′S, 153°24′E), flat immediately at the edge of the slope with *Triglochin*, surface sediment (0–2 cm depth), 17.02.2005, I. Bartsch. PARATYPES: QM-S83658, ♀, collection data as above. QM-S83659, ♀, collection data as above. SMF, ♂, collection data as above. ZMH, ♂, collection data as above. OTHER MATERIAL. SMF, ♀, Adam's Beach, Dunwich, North Stradbroke Is., Moreton Bay (c: 27°30′S, 153°24′E), flat immediately at the edge of the slope with *Triglochin*, 3–5 cm sediment depth, 17.02.2005, I. Bartsch. QM-S83660, ♂, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay, sediment from middle beach slope, about 20 cm sediment depth, 18.02.2005, I. Bartsch. ZMH, ♀, ♂, collection data as above. IBC, 2 ♀♀,
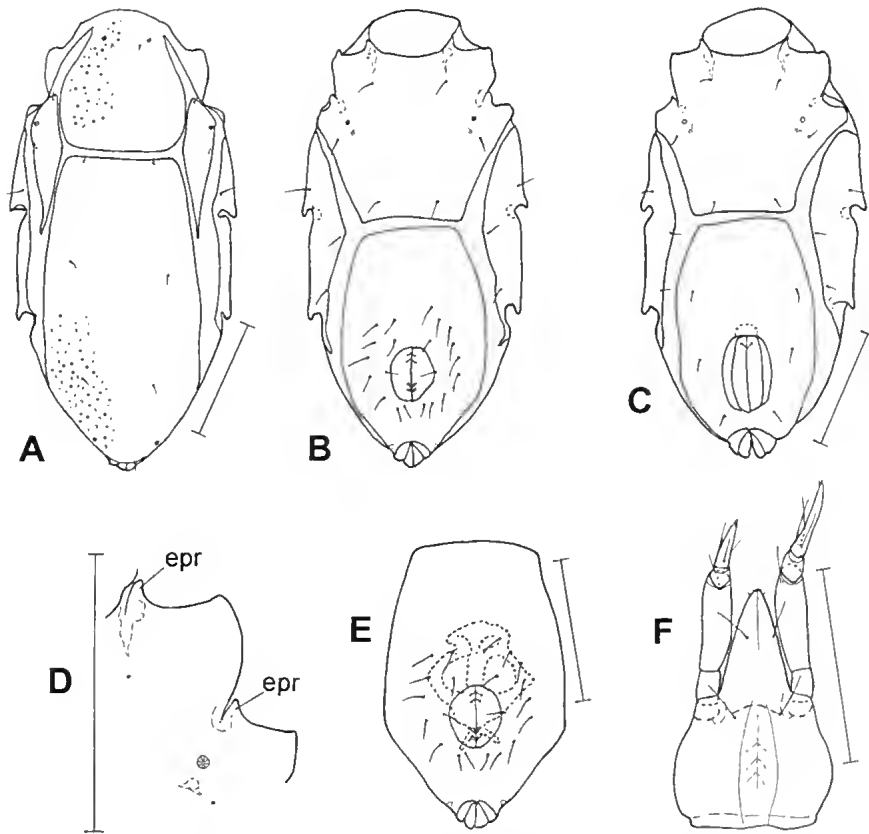
FIG. 2. *Copidognathus psammobius* sp. nov.; **A**, Idiosoma, dorsal, ♂; **B**, idiosoma, ventral, ♂; **C**, idiosoma, ventral, ♀; **D**, left AE, ♂; **E**, genitoanal plate, ♂; **F**, gnathosoma, ventral, ♂. Scale line = 50 μm (epr = epimeral process) (A, B, D, E, holotype QM-S83657; C, paratype QM-S83658; F, paratype SMF).

North Stradbroke I., Moreton Bay, sandy slope near Polka Point (off the Moreton Bay Research Station), c. 27°30'S, 153°23'E, upper beach area, 20 cm sediment depth, 11.02.2005, I. Bartsch.

Diagnosis. Length of female 185–213 μm, of male 180–216 μm. Dorsal plates very delicately pitted, ventral plates finely punctate. Opposing margins of AD and PD and AE and GA truncate. OC narrow, extending beyond insertion of leg III. With pointed epimeral processes. Female GA with anterior pair of pgs close to margin of plate; ovipositor short. Male with 20–21 pgs. Rostrum not reaching to end of P-2. Tectum arched. Leg I wider and longer than leg II. Tarsus I with enlarged lateral fossa membrane. Leg chaetotaxy (solenidion included, pas and famulus excluded): leg I, 1, 2, 4, 3, 6–7, 7; leg II, 1, 2, 4, 3, 6–7, 4; leg III, 1, 2, 2, 2, 5, 4; leg IV, 0, 2, 2, 3, 5,

3. Tibiae I to IV with 2, 2, 1, 1 bipectinate setae. Claws of tarsi II to IV with few large tines.

Description. *Male.* Length of idiosoma 180–216 μm, length of holotype 192 μm, width 94 μm. Dorsal plates evenly punctate and with scattered pits (Fig. 2A), each pit 1–2 μm in diameter; otherwise without marked ridges and ornamentation. With three small spots of black eye pigment, one beneath AD and one beneath each of OC. Anterior margin of AD arched, posterior margin truncate; length of plate 57 μm, width 51 μm. Gland pores at 0.2. OC slender, elongate; their length 58 μm, width 16 μm, posteriorly pointed and extending beyond insertion of leg III. Gland pore and adjacent pore canaliculus in lateral margin. Cornea absent. Length of PD 128 μm, width 67 μm; anterior margin truncate. Gland pores at 0.9. Dorsal idiosomatic setae slender, short. Pair of ds-1 on AD slightly posterior to
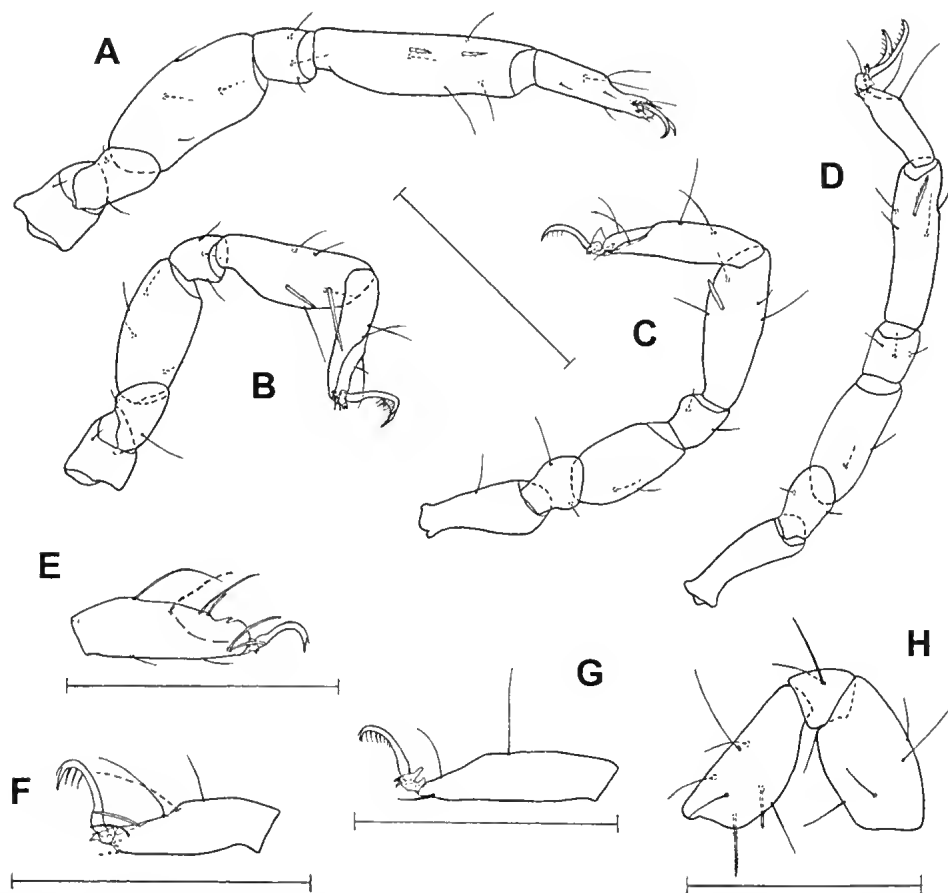
FIG. 3. *Copidognathus psammobius* sp. nov.; **A**, Leg I, ventromedial, ♂; **B**, leg II, medial, ♂; **C**, leg III, medial, ♂; **D**, leg IV, ventromedial, ♂; **E**, tarsus I, lateral, ♀ (medial fossary seta in broken line, medial parambulacral setae and claw omitted); **F**, tarsus II, lateral, ♂ (medial fossary seta and parambulacral seta in broken line); **G**, tarsus IV, lateral, ♀ (medial fossary seta, parambulacral seta and claw omitted), **H**, telofemur to tibia II, lateral, ♂. Scale line = 50 μm (A–D, holotype QM-S83657; E, G, paratype QM-S83659; F, H, QM-S83660).

gland pores; ds-2 in anteromedial corner of OC; ds-3 to ds-5 on PD as illustrated; adanal setae on anal cone.

Surface of ventral plates delicately punctate. Length of AE 66 μm, width 83 μm; epimeral processes I and II lamelliform (Fig. 2B, D). Pair of epimeral pores small, four marginal tines constricting the opening (Fig. 2D). Plate with three pairs of setae. Posterior margin of AE truncate. PE with one dorsal and three ventral setae; length 93 μm; PE extending beyond insertion of leg IV. Anterior margin of GA truncate; length of plate 101 μm, width 64 μm. Length of GO 22 μm, width 17 μm. Interval between GO and anterior margin

of GA 2.1 times length of GO. With 10–11 pgs on either side of GO. Spermatopositor extending slightly beyond anterior pgs (Fig. 2E).

Length of gnathosoma 56 μm, width 39 μm, with two pairs of maxillary setae. Rostrum in ventral aspect triangular (Fig. 2F), not extending to end of P-2, somewhat shorter than gnathosomal base. Rostral sulcus extending just beyond apical pair of maxillary setae. Tectum arched. P-2 with one dorsal seta; no seta on P-3; P-4 with three setae in basal whorl, setula and two spurs at its tip.

Leg I longer than leg II (Fig. 3A and B). Tibiae I and II slightly longer than the legs telofemora,

tibiae III and IV distinctly longer than telofemora (Fig. 3C and D). Telofemora I and II 1.7 times longer than high; telofemora III and IV almost twice as long as high. Leg chaetotaxy (holotype, solenidion included, pas and famulus excluded): leg I, 1, 2, 4, 3, 6, 7; leg II, 1, 2, 4, 3, 6, 4; leg III, 1, 2, 2, 2, 5, 4; leg IV, 0, 2, 2, 3, 5, 3. Tibia I ventrally with two short, delicately bipectinate setae and one smooth and slender seta. Apical one of the two bipectinate setae on tibia II distinctly longer than basal seta. Tibiae III and IV each with one short, bipectinate and one smooth, slender seta. Apex of tarsus I with large lateral membrane; medial membrane as well as fossa membranes of the other legs inconspicuous. On tarsus I one of the two distal fossary setae inserted at base of claw fossa, the other on lateral membrane (Fig. 3E); solenidion immediately adjacent, 5 μm long. Venter of tarsus I with three setae and apical pair of doubled pas. Solenidion on tarsus II 10 μm long, in dorsolateral position and close to parambulacral seta (Fig. 3F); tarsus II with pair of pas singlets. Tarsi III and IV with four and three dorsal setae, respectively, two distal setae paired, inserted close to tip of tarsi; apex with pair of pas (Fig. 3G).

Claws slender, on tarsus I shorter than on following tarsi. Claws with accessory process, on tarsi II to IV with few long and slender tines. Median claw bidentate.

Female. Length of idiosoma 185–213 μm. Dorsal aspect same as that of male. GA longer than AE, anterior margin truncate (Fig. 2C). Setae pgs-1 and pgs-2 close to lateral margins, pgs-1 somewhat anterior to the level of insertion of leg IV. GO in posterior portion of GA, distance to anterior margin of GA equalling 1.5 times length of GO. Ovipositor only sligthly passing beyond margin of GO.

Variations. On tibiae I and II both three and four dorsal setae were found. In one male the tibiae of one side had three on the other side four dorsal setae (Fig. 3H). Twelve of the tibiae I examined had 3/3 dorsal/ventral setae, six tibiae the combination 4/3, and in one female, one of the tibiae I had unilaterally 3/2 dorsal/ventral setae, one of the bipectinate ventral setae was lacking, the other tibia had 3/3 setae. On tibia II the combinations 3/3 and 4/3 dorsal/ventral

setae were found nine and five times, respectively.

Remarks. Species similar to *C. psammobius* are *C. mirus* Bartsch, 1984, *C. consobrinus* Bartsch, 1991, *C. cribellus* Bartsch, 1993, *C. laeviusculus* Bartsch, 1993, *C. lepidus* Bartsch, 1977, and *C. majorinus* Bartsch, 1993. They are all known from the Indo-Pacific area (Bartsch 1977, 1984, 1991, 1993), and are small, the idiosoma less than 240 μm, the surface of the dorsal plates lacks costae or clearly delimited porose areolae, and any ornamentation, if present, is either weak or rather uniform. The opposing margins of the AD and PD are truncate and the OC elongate and slender.

Copidognathus lepidus is recorded from the Galapagos Islands (Bartsch 1977). In contrast to *C. psammobius* and the other above mentioned species, the first pair of gland pores are inserted immediately adjacent to each other. Furthermore the tibiae bear large, pointed articular membranes, on the female GA the pgs are far from the lateral margin of the plate, and the ovipositor is large, extending far beyond the anterior margin of the GO. The length of the species is 199–204 μm.

Copidognathus consobrinus, from southern China (Bartsch 1991), has a length of 174–187 μm, its dorsal plates are uniformly punctate, not pitted, the OC are not conspicuously prolonged, in the males the perigenital setae are close to the GO, and tibia I has a cylindrical base that rapidly increases in height.

Copidognathus mirus is known from the Philippines (Bartsch 1984). The idiosomal length is 210 μm. Its dorsal plates are uniformly punctate, the OC are tail-like prolonged but shorter than in *C. psammobius*. In the single specimen of *C. mirus* studied the PE have no more than three setae, one dorsal, two ventral, the epimeral pores have a wide internal sacculus, opening on the AE with a slit, and the pair of genital acetabula are enlarged and sacculiform. The function of the enlarged epimeral pores and genital acetabula is not known and consequently it cannot be excluded that these structures are enlarged only during periods of activity.

The three psammophilous species *C. cribellus*, *C. laeviusculus* and *C. majorinus* are from sandy shores of Western Australia (Bartsch 1993). Delicate rosette pores uniformly cover the dorsal

plates of *C. cribellus*, and this ornamentation separates *C. cribellus* from *C. psammobius* and the other above mentioned species. The idiosomal length of *C. cribellus* is 217–232 μm. The length of *C. laeviusculus* is 184–192 μm; its dorsal plates are almost smooth, the ds-1 stand adjacent to the gland pores, the OC are rather wide and the gland pore is near the middle of the plate, the margins in the posterior portion of the AE are almost parallel-sided, in both females and males the epimeral pores and genital acetabula are enlarged, and tibia I is not cylindrical as in *C. psammobius* but conspicuously widened near the segments middle. *Copidognathus majorinus* measures 218–224 μm; its plates are uniformly and delicately punctate, the OC are shorter than in *C. psammobius*, both females and males have enlarged epimeral pores and genital acetabula, the pgs on the male GA are arranged in two lines close to the lateral margin of the plate, and the tibiae bear articular lamellae.

Copidognathus pygmaeus Bartsch, 1980 is a species from a sandy shore of Massachusetts, United States Atlantic coast (Bartsch 1980). It is similar to the above mentioned species but the dorsal plates show delicately delimited areolae in which the plates are punctate and their surface bears foveae; and each OC bears one distinct and one weakly delimited cornea. *C. pygmaeus* reaches 217 μm in length.

Etymology. The name is derived from the Greek bios (to live), combined with psammos (sand), and refers to its lifestyle.

Distribution & Biology. *Copidognathus psammobius* is at present known from Moreton Bay, Queensland, Australia. The species was extracted from sediment of a slope, from the ground water table, and the adjacent flat, both habitats under strong freshwater influx, as well as from a beach without marked freshwater input.

Copidognathus cooki Bartsch, 2003

Copidognathus cooki Bartsch, 2003: 12–14, figs 1–17.

Material Examined. QM-S83661, ♀, ♂, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30′S, 153°24′E), tidal flat immediately at the edge of the slope with *Juncus* and *Triglochin*, surface sediment, 17.02.2005, I. Bartsch. IBC, ♀, collection data as above. IBC, ♀, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay, mud flat with *Catenella* and *Bostrychia* (Rhodophyta). IBC, ♀, ♂, Myora Conservation Park,

north of Dunwich, North Stradbroke I., Moreton Bay (c. 27°29′S, 153°24,5′E), from mudflat with *Calloglossa* (Rhodophyta) near a freshwater seepage, 22.02.2005, I. Bartsch.

Diagnosis. Length of female 264–281 μm, of male 269–294 μm. With three large spots of dark eye pigment. Dorsal plates reticulate-foveate. Slightly raised areolae with weakly developed rosette pores, each with wide fovea-like ostium and very delicate canaliculi; reticulate ornamentation of raised areolae similar to that of remaining areas. AD with three porose areolae, anterior areola extending into small frontal spine, posterior areolae elongate. PD with single pair of costae which are weakly developed and one rosette-pore wide, rarely two pores wide. OC posteriorly slender, elongate. Setae ds-2 in anteromedial margin of OC; ds-3 to ds-5 on PD. Ventral plates reticulate, each polygon with numerous delicate canaliculi. Opposing margins of AE and GA wide, truncate. Distance between anterior margin of female GA and GO equalling 1.3 times length of GO. Ovipositor extending slightly beyond GO. Male GA with 25–29 pgs. Spermatopositor large, extending beyond GO by almost length of GO. Rostrum not reaching end of P-2. Tectum triangular. Trochanters III and IV dorsally pointed. Telofemora short, from I–IV with 5, 5, 2, 2 setae. Tibiae I to IV ventrally with 2, 2, 1, 1 bipectinate setae, and 1, 1, 1, 1 slender and smooth setae. Tarsi III and IV with four and three setae. Claw pectines with distinct tines.

Remarks. Some of the mites had thecate suctorians attached; theca length 27–35 μm, stalk 25 μm.

Copidognathus cooki is classified a brackish water species which can survive fluctuations in salinity from brackish to fresh (Bartsch 2003). The type material was collected in the Swan River, Perth, Western Australia, at 2–6 ‰ salinity; in an area sometimes reached by upstream saltwater wedges of more than 24 ‰.

At the Adam's Beach and Myora Conservation Park collecting sites, *C. cooki* was present amongst the surface sediment of the tidal flat, adjacent to the shoreline freshwater seepage. During low tide the salinity in the muddy surface layer was reduced to 0–3‰. The species was also found on the mangrove mud flat at 18‰ (at low water), amongst *Calloglossa* sp., together with an *Aganopsis* species. At high tide, the salinity ranged from 28 to more than 30‰.
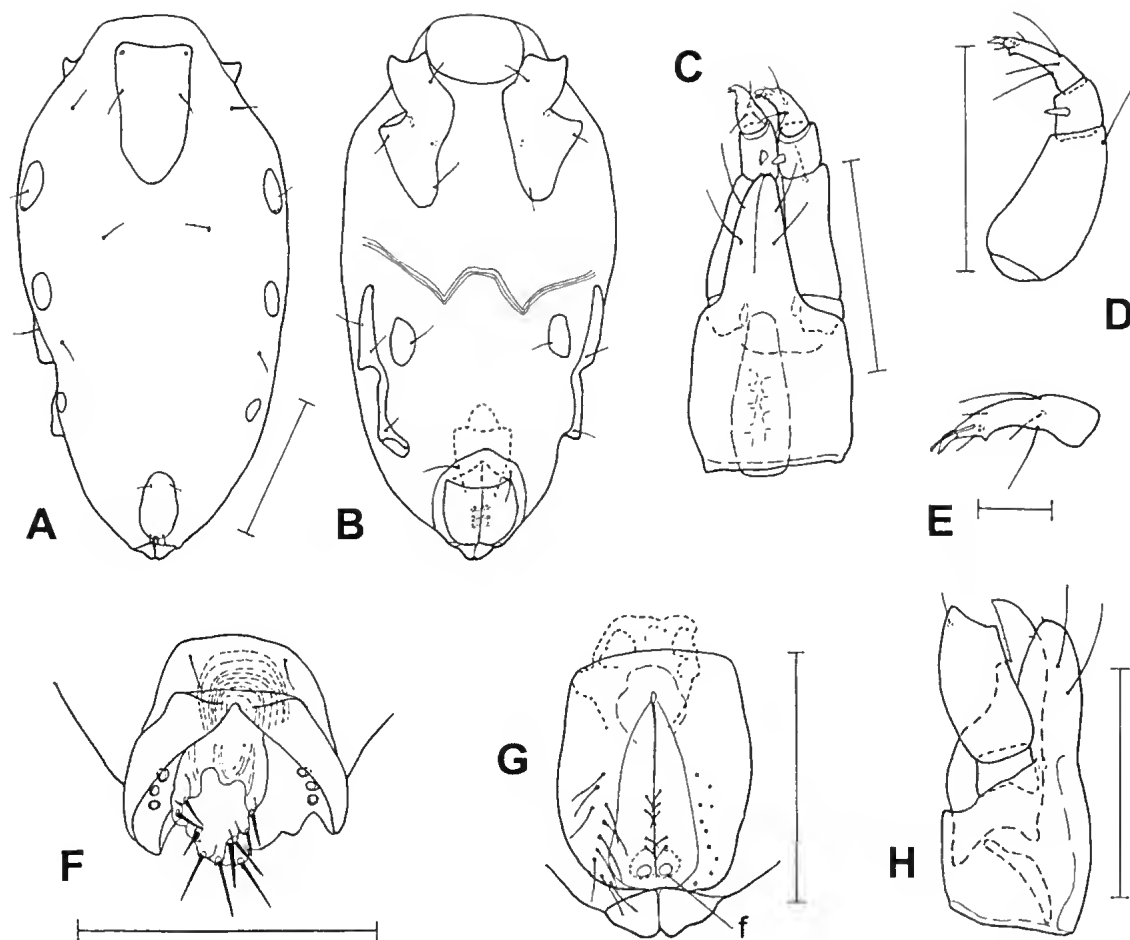
FIG. 4. *Halacaroides australiensis* sp. nov.; **A**, Idiosoma, dorsal, ♀; **B**, idiosoma, ventral, ♀; **C**, gnathosoma, ventral, ♀; **D**, P-2 to P-4, medial, ♀; **E**, P-4, lateral, ♀; **F**, genitoanal plate and ovipositor, ♀; **G**, genitoanal plate, ♂; **H**, gnathosoma, lateral, ♂. A–D, F–H, scale line = 50 μm, E, scale line = 10 μm. (f, fovea with genital acetabula) (A, B, D, E, holotype QM-S83662; C, paratype ZMH; F, paratype QM-S83663; G, paratype QM-S83664; H, paratype ZMH).

In samples taken during a previous Marine Biological Workshop in Esperance, Western Australia, *C. cooki* was regularly present in Bandy Creek, in shallow water substrata, amongst sand rich in organic material and *Polyphysa* (Chlorophyta) covered by debris (unpublished record). It was the only halacarid present in the samples. At the end of a dry summer the salinity in that creek amounted to 14–18‰ .

Distribution & Biology. Known from both southeastern Australia, from Moreton Bay, Queensland, and south-western Australia from the Swan River, Perth, and Bandy Creek, Esperance, Western Australia. All records are from brackish water habitats, none from an exclusively marine shore.

Halacaroides Bartsch, 1981

Type species: *Halacaroides angustus* Bartsch, 1981.

Halacaroides australiensis sp. nov.
(Figs 4A–H, 5A–I)

Material Examined. QM-S83662, HOLOTYPE ♀, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30′S, 153°24′E), upper slope, ground water table, 18.02.2005, I. Bartsch. PARATYPES. QM-S83663, ♀, collection data as above. QM-S83664,

♂, collection data as above. QM-S83665, deutonymph, collection data as above. SMF, ♂, collection data as above. ZMH, ♀, collection data as above. ZMH, ♂, collection data as above. IBC, ♀, ♂, collection data as above.

Diagnosis. Length of idiosoma 170–188 μm. Dorsal and ventral plates small, delicate. Anterior epimeral plate longitudinally divided. PE divided into marginal and small ventral portion. Marginal portion with three setae, ventral portion with one seta. Female with single pair of pgs; no sgs. Male GP with 10 pairs of pgs; genital sclerites with four to five pairs of sgs and posteriorly a pair of foveae. Gnathosoma slender, rostrum almost reaching to end of P-2. Palps with one seta on P-2, one medial spine on P-3, and three setae in basal whorl of P-4. Leg I much longer than leg II and longer than following legs. Leg chaetotaxy (pas excluded, solenidion and famulus included): leg I, 1, 2, 5, 5, 8, 8; leg II, 1, 2, 4, 5, 5, 4; leg III, 2, 2, 3, 3, 6, 4; leg IV, 1, 2, 3, 3, 5, 3. Tarsus III with lateral pas removed from tip of tarsus, tarsus IV with both pas removed.

Description. *Female.* Length of idiosoma 177–187 μm (from anterior margin of AD to end of anal cone), that of holotype 180 μm, width 95 μm. Dorsal plates delicate; integument between plates with parallel striae. Length of AD 48 μm, width 27 μm. Pair of gland pores near anterior margin of plate. Dorsum with three pairs of sclerites (Fig. 4A), 17, 15 and 9 μm in length, with delicate internal markings from muscle attachment. First pair of sclerites with delicate pore (pore canaliculus). PD much smaller than AD, its length 25 μm, width 12 μm. All dorsal idiosomal setae short. Pair of ds-1 in anterior half of AD. Pair of ds-2 in striated integument almost at the level of ds-1. One pair of setae laterally on anterior pair of sclerites, one pair dorsally in striated integument, and one pair of setae laterally between two posterior pairs of sclerites. PD with pair of dorsal setae and adanal setae.

AE longitudinally divided, length 38 μm, each half with three setae; no epimeral pores present (Fig. 4B). PE divided, length of marginal PE 62 μm. Marginal PE with one dorsal and two ventral setae, ventral PE with single seta. Length of GA 38 μm, width 29 μm. GO almost as large as genital plate; anterior part of GO covered by lamella. GA with single pair of pgs. Ovipositor in rest extending beyond GA. Three pairs of

internal genital acetabula on inside of genital sclerites. Ovipositor with at least five pairs of slender genital spines (Fig. 4F).

Length of gnathosoma 70 μm, width 35 μm. Rostrum elongate, almost reaching end of P-2 (Fig. 4C, H). Tectum excavate. Both pairs of maxillary setae on rostrum, basal pair in about middle of rostrum. Tip of rostrum with two pairs of small rostral setae (Fig. 4H). Rostral sulcus extending backward beyond basal pair of maxillary setae. Palps four-segmented, P-2 with single dorsal seta, P-3 with stout, short medial spine (Fig. 4D). P-4 slightly curved, with three setae in a basal whorl; posterior half of P-4 with two setulae, one eupathid seta, a claw and a minute protuberance (Fig. 4E).

Legs slender, leg I much longer than leg II and longer than legs III and IV. Genu of leg I almost as long as telofemur but shorter than tibia I (Fig. 5A). Genua of legs II to IV shorter than telofemora. Tibia and telofemur II almost equal in length (Fig. 5B); tibiae III and IV longer than telofemora (Fig. 5C, D). Telofemur I 2.4 times longer than high, telofemora II to IV 2.0–2.1 times longer than high. Tarsus I with large lateral fossa membrane (Fig. 5E); medial membrane absent. The other tarsi with narrow medial and slightly wider lateral fossa membranes. Leg chaetotaxy (pas excluded; solenidion and famulus included): leg I, 1, 2, 5, 5, 8, 8; leg II, 1, 2, 4, 5, 5, 4; leg III, 2, 2, 3, 3, 6, 4; leg IV, 1, 2, 3, 3, 5, 3. All telofemora with a ventral seta. Genu I with pair of short ventral setae, genua II to IV with one ventral seta each. Tibia I with two pairs of slender ventral setae; tibiae II to IV with 2, 3, 2 ventral setae. These setae of tibiae II and IV long, stout and widened. Tarsi I to IV with 3, 0, 0, 0 ventral setae and each ending with pair of pas. Solenidion on tarsus I in dorsolateral position, 9 μm in length, famulus immediately adjacent, 8 μm long (Fig. 5E). Solenidion on tarsus II clavate, 7 μm long, inserted on narrow medial fossa membrane (Fig. 5F). Tarsus III with a short, eupathid dorsolateral seta (Fig. 5G). All tarsi with slender dorsal fossary seta, followed by paired, somewhat wider setae. Tarsi I and II with eupathid pas; on tarsus III medial pas eupathid, lateral pas long, slender, in more proximal position than medial pas; on tarsus IV both pas long, slender and in a proximal position, medial pas slightly closer to tip of tarsus than lateral pas.
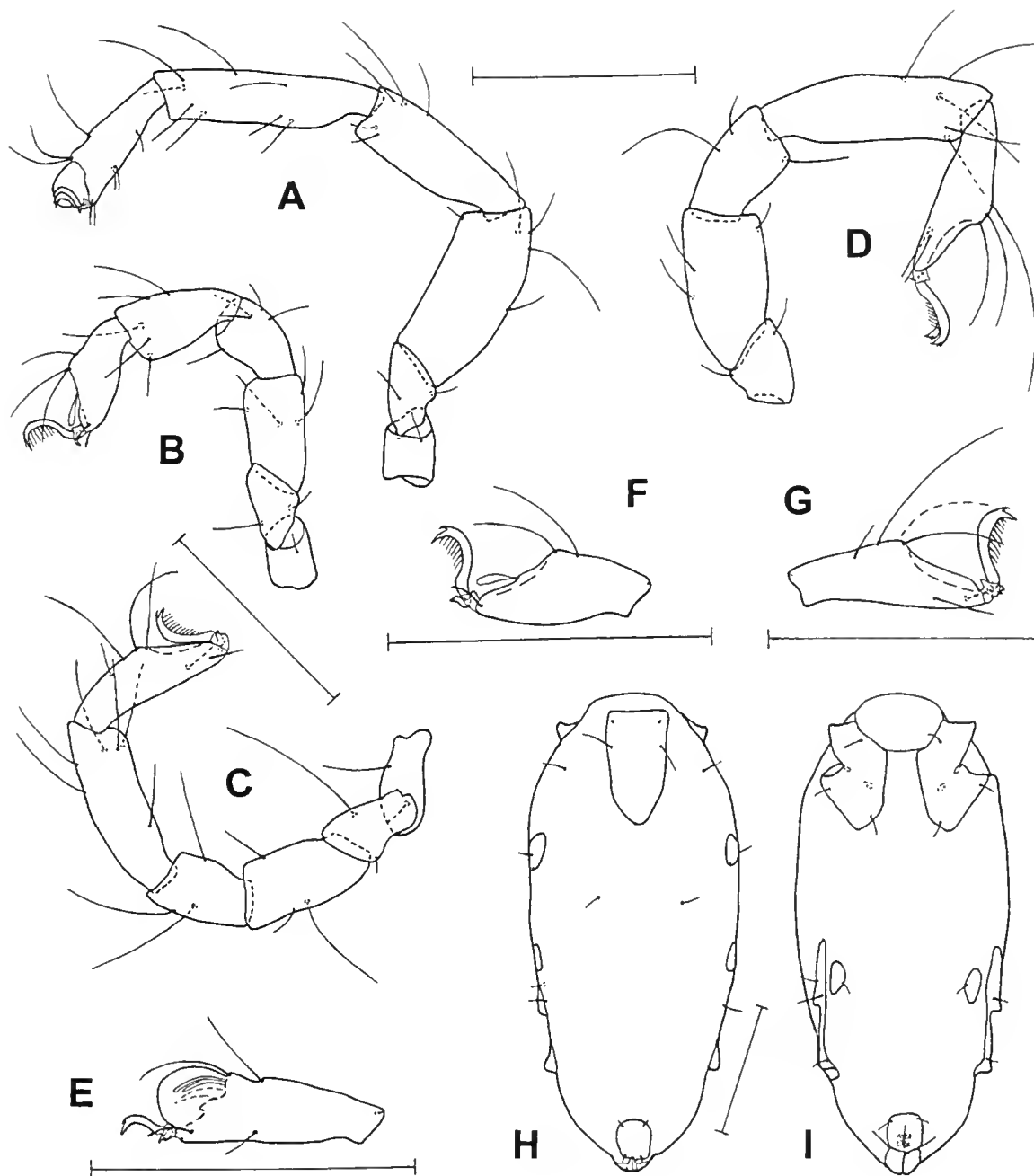
FIG 5. *Halacaroides australiensis* sp. nov.; **A**, Leg I, medial, ♂; **B**, leg II, medial, ♂; **C**, leg III, medial, ♂; **D**, basifemur to tarsus IV, medial, ♂; **E**, tarsus I, lateral, ♀ (medial setae and claw omitted); **F**, tarsus II, medial, ♂ (lateral setae and claw omitted); **G**, tarsus III, lateral, ♂ (medial setae in broken line); **H**, idiosoma, dorsal, deutonymph; **I**, idiosoma, ventral, deutonymph. Scale line = 50μm (A–D, F, G, paratype QM-S83664; E, paratype QM-S83663; H, I, paratype QM-S83665).

Claws on leg I smaller than on following legs. All claws with accessory process, those of tarsi II to IV with long, coarse tines. Median claw small, bidentate.

Male. Length of idiosoma 170–188 μm. Length of GA 82 μm, width 40 μm. Plate with ten pairs of pgs (Fig. 4G). Genital sclerites long and slender, indistinctly delimited from GA. Genital sclerites with four (and five) short sgs and posteriorly with pair of foveae, each including three genital acetabula and opening to exterior via 3 μm-wide pore. Spermatopositor extending beyond GA.

Deutonymh. Length 177 μm. Dorsal aspect (Fig. 5H) and outline of ventral plates AE and PE (Fig. 5I) similar to those of female. Number and arrangement of setae on dorsum, AE and PE same as in adults. Genital plate small, quadrangular, with pair of pgs and two pairs of internal genital acetabula. Leg chaetotaxy (pas excluded, solenidion and famulus included): leg I, 1, 2, 5, 5, 8, 8; leg II, 1, 2, 4, 5, 5, 4; leg III, 2, 2, 3, 3, 6, 4; leg IV, 1, 2, 2, 3, 5, 3. No ventral seta on telofemur IV.

Remarks. Two species were known to belong to *Halacaroides, H. angustus* Bartsch, 1981 and *H. brevocularis* Bartsch, 1981, both recorded from southern South America (Bartsch 1981). The present species differs in several characters, but these are not considered generically significant, and thus do not prevent the Australian species to be placed in *Halacaroides*.

The characters are:

1) The dorsum of *H. australiensis* bears seven instead of six pairs of idiosomal setae — the seta on the anterior pair of the lateral sclerites is expected to replace a gland pore. Setae associated with or replacing gland pores are known in species of the genera *Rhombognathides, Metarhombognathus* and *Lohmannella.*

2) The AE are not fused but longitudinally divided — in other genera, viz. *Anomalohalacarus* and *Metarhombognathus* (deutonymph), some species have a divided others a uniform AE. They are congeners despite the shape of their AE.

3) The females have a single pair of perigenital setae — three pairs of perigenital setae are present on the female GA of *H. angustus* and *H. brevocularis,* and this number is the most common state within halacarids, but both lower

and higher numbers are documented, e.g. in *Rhombognathus.*

4) In *H. australiensis* males, the genital acetabula are moved to a posterior fovea — a similar situation is found in males of a few *Halacarellus* species which live in sand at at least periodically reduced salinity.

5) Trochanter III bears two setae — a re-examination of the type material of *H. angustus* showed that the telofemora III bear two setae, one in lateral and one in dorsal position. Furthermore, intrageneric differences in this character state occur, some *Halacarellus* species have one, others two setae on trochanter III.

6) *Halacaroides angustus* and *H. brevocularis* have a ventral seta on tarsus II, *H. australiensis* none — in several halacarid genera the number of ventral setae on tarsus II is known to vary.

Etymology. This is the first record from Australia, hence the name *australiensis.*

Distribution & Biology. Moreton Bay, Queensland. *Halacaroides australiensis* was only found in a beach strongly influenced by freshwater. Sediment from a small slope near the Moreton Bay Research Station, Dunwich, contained *Copidognathus psammobius* and *Anomalohalacarus* sp. but no *H. australiensis.*

Limnohalacarus Walter, 1917
Type species: *Halacarus wackeri* Walter, 1917.

Limnohalacarus billabongis Bartsch, 1999
Limnohalacarus billabongis Bartsch, 1999: 446–449, figs 3A–G, 4A–F, 5A–D.

Material Examined. QM-S83666, ♀, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30'S, 153°24'E), tidal flat, subsurface sediment in 3–5 cm depth, 18.02.2005, I. Bartsch. IBC, 4 ♀♀, 1 deutonymph, collection data as above.

Diagnosis. Length of female 262–300 μm. Dorsal plates reticulate, ventral plates uniformly punctate. OC mostly undivided. All ventral plates fused. Area representing GA with 9–11 genital acetabula, one pair of pgs anterior to row of acetabula and two pairs close to GO; genital sclerites with two pairs of sgs. P-2 with one spur-like and one long, slender seta. Leg chaetotaxy (pas excluded, solenidion included): leg I, 1, 4, 4, 6, 8, 5; leg II, 1, 4, 4, 7, 4; leg III, 1, 2, 3, 4, 7, 4; leg IV, 0, 1, 3, 3, 6, 3. Tibia I with three ventral setae, two bristle-

like, one slender; tibia II with two ventral setae, one slightly barbed; tibia III with two pairs of ventral setae, two of them smooth, two bipectinate, tibia IV with single pair of smooth ventral setae. Solenidia setiform, all in dorsolateral position. Claws with distinct pectines. Tines on claw I long, on tarsi II to IV shorter, basal tines on small lamellar process.

Supplementary Description. In several adult specimens, OC partly divided by lateral wedge of striated integument extending transversely between triangular part around gland pore and larger anterior part of OC. One female unilaterally with single sgs on genital sclerite, another female unilaterally with four pgs.

Length of deutonymph 270 μm. OC completely divided by transverse fissure of striated integument.

Remarks. The present specimens differ from the type material in that the genital sclerites bear mostly two pairs of sgs (a single pair in the type specimens) and tibia I three ventral setae (four in the types).

Distribution & Biology. Queensland and Northern Territory, Australia. The first records were from Kakadu National Park, NT (Bartsch 1999). *Limnohalacarus billabongis* is primarily a freshwater mite.

Lobohalacarus Viets, 1939

Type species: *Walterella weberi* Romijn & Viets, 1924.

Lobohalacarus weberi (Romijn & Viets, 1924)

Walterella weberi Romijn & Viets, 1924: 217, figs 3–6.
Lobohalacarus weberi Viets, 1939: 506.

Material Examined. QM-S83667, ♀, deutonymph, Adam's Beach, Dunwich, North Stradbroke I., Moreton Bay (c. 27°30′S, 153°24′E), tidal flat, subsurface sediment in 3–5 cm, 18.02.2005, I. Bartsch. IBC, larva, Adam's Beach, edge of lower slope and tidal flat, surface sediment, 17.02.2005, I. Bartsch. IBC, 2 ♀♀, swamp area near Adam's Beach, freshwater pond, 18.02.2005, I. Bartsch, found together with the freshwater halacarids *Ropohalacarus uniscutatus* (Bartsch 1982) and *Soldanellonyx monardi* Walter, 1919.

Diagnosis. Length of female 350–360 μm, with frontal spine. Dorsal plates punctate and uniformly pitted. OC elongate. Dorsum with seven pairs of idiosomal setae. Ventral plates fused to a shield, area of PE with one dorsal, one lateral and one ventral seta; area of GA with five pairs of pgs. Genital sclerites with two to three pairs of genital acetabula. Gnathosoma slender. P-2 with one seta. P-3 with medial spine, P-4 with three setae in basal whorl. Leg I longer than leg II. Length of genu I similar to that of the leg's telofemur. Genu and tibia I ventrally with one spine, one bristle and two spines, two bristles, respectively. Tibiae II to IV ventrally with 2, 2, 1 bipectinate setae and 1, 1, 2 smooth bristles. Telofemora III and IV with 2/1 and 2/0 dorsal/ ventral setae, respectively. Tarsus I with large lateral fossa membrane. Solenidion on tarsus I in dorsolateral, on tarsus II in dorsomedial position. One of three ventral setae of tarsus I spur-like. Tarsi II to IV with 4/1, 4/1 and 3/1 dorsal/ ventral setae, respectively.

Supplementary Description. The female from the subsurface sediment of the tidal flat has three pairs of genital acetabula, while the two females from the freshwater pond have two pairs.

Idiosomal length of larva 154 μm. AD with frontal spine.

Remarks. *Lobohalacarus weberi* appears highly variable in characters such as the number and shape of setae on the legs and around the GO, and the number of genital acetabula on the genital sclerites. The present females are within the range of variation shown by European *L. weberi*. Data from Bartsch (1995) and from recent studies on freshwater halacarids of North America, from British Columbia to Newfoundland and California to Georgia (material forwarded by Dr. I. Smith, Ottawa; unpublished), showed that in most collections a range of character states exists, also unilateral combinations, though in a given population often one variant clearly dominates. The variants are thought to be intraspecific rather than representing several cryptic species.

Distribution & Biology. *Lobohalacarus* species are regularly found in the Australian groundwater (Harvey 1988; Proctor 2001; Boulton & Harvey 2003; Boulton *et al.* 2004). The first records of *L. weberi* were from Europe. When described subspecies are included, *L. weberi* must be considered a wide-spread species with records from Europe, North Africa, North America, Japan, Australia (present record), New Zealand, and

the Hawaiian and Tristan da Cunha Islands (Bartsch 1995, 2007).

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Sea-spiders (Arthropoda: Pycnogonida) from Moreton Bay, Queensland

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ABSTRACT

Sampling of the littoral and sublittoral benthos around Moreton Bay, Queensland, Australia, undertaken in February 2005, revealed, *inter alia*, eighty pycnogonid specimens representing thirteen species from nine genera. Only eight of these species had been recorded previously from Australia, viz. *Achelia shepherdi*, *A. assimilis*, *Endeis flaccida*, *Ascorhynchus longicollis*, *Pseudopallene reflexa*, *Anoplodactylus cribellatus*, *A. tubiferus* and *Nymphon molleri*. An *Ascorhynchus* species closest to the New Zealand species *A. insularum* (tentatively, based on a subadult), the Tanzanian species *Propallene ardua* and the allegedly Caribbean-Northeast Atlantic-Mediterranean species *Callipallene emaciata* sensu stricto are newly recorded for Australia, as are previously undescribed species of *Oropallene* and *Nymphon*. ❑ Pycnogonida, Queensland, Australia, Achelia, Anoplodactylus, Ascorhynchus, Callipallene, Endeis, Nymphon, Oropallene, Propallene, Pseudopallene.

Sampling of the littoral and sublittoral benthos around Moreton Bay, Queensland, Australia, was undertaken in February 2005 in order to characterise the smaller marine arthropod fauna of this region, including pycnogonids. In the event, although few pycnogonids were collected, they included two previously undescribed species, new records for Australia, or range extensions of under- recorded species.

Previous records of pycnogonids from eastern Australia are sporadic, predominantly reported by Clark (1963), who listed the earlier literature for Australia; Stock (1973a, b) recorded species from Victoria and South Australia; Staples (1979, 1982) reported on pycnogonids from Queensland (north of Brisbane), Victoria and South Australia, and subsequently (Staples 1997) collated the species from South Australia, with additional reporting on South Australian species in Staples (2004); Child (1990), and recently Lee & Arango (2003) and Arango (2003) reported on pycnogonids from the Great Barrier Reef, and the last reviewed all the previous Australian pycnogonid recording, while Child (1975) and Bamber (2005) reported on pycnogonids from Western Australia.

METHODS

Collecting methods were by hand (diving) and by various sampling gears, notably a standard 0.1m^2 van Veen grab and a spanner-crab dredge. Other sampling was opportunistic and non-quantitative. Position fixing was by GPS. All specimens were collected under Queensland Marine Parks Permit No. QS2005/CVL1057.

During the 2005 workshop, Peter Davie undertook a wider grab sampling survey south of Peel Island, in southern Moreton Bay. Material from these samples were kindly initially identified by Claudia Arango. Station details are given in Table 1; these samples are referred to in the text as 'MBWS Stn #'.

Specimens were sorted live to allow observation of colouration, then fixed in 100% ethanol or 75% methanol. Drawings were all done using a camera lucida. Measurements are axial (Fry & Hedgpeth 1969), dorsally on the trunk and laterally on the appendages. Voucher and type-material has been lodged in the collections of the Queensland Museum (QM) and The Natural History Museum, London (NHM). The higher taxonomy

Table 1. Station details for the MBWS survey of February 2005, south of Peel Island, Moreton Bay, Queensland.

Stn	Latitude	Longitude	Depth (m)	Date
1	27° 31.25′	153° 22.00′	5.7	17/02/2005
2	27° 31.25′	153° 21.85′	5.8	17/02/2005
3	27° 31.25′	153° 21.65′	5.6	18/02/2005
4	27° 31.53′	153° 21.44′	5.1	20/02/2005
5	27° 31.53′	153° 21.70′	5.7	20/02/2005
6	27° 31.55′	153° 20.80′	7.7	18/02/2005
7	27° 31.48′	153° 20.72′	8.2	18/02/2005
8	27° 31.48′	153° 20.48′	8.4	18/02/2005
10	27° 31.68′	153° 20.54′	7.6	18/02/2005
13	27° 31.98′	153° 20.62′	6.2	20/02/2005

is based on Arnaud & Bamber (1987) as modified by Bamber (2007).

Terminology: larvae are specimens without an open anus; juveniles are specimens without four fully developed pairs of legs; subadults are specimens with four fully developed pairs of legs but without fully developed ovigers (where these are present). Terminology of the cuticular ornamentation follows that of Bamber (2004).

SYSTEMATICS

Family AMMOTHEIDAE Dohrn, 1881

Achelia Hodge, 1864

Achelia shepherdi Stock, 1973

Achelia shepherdi Stock, 1973b, 92–95, figs 1, 2; Child, 1975, 22–24, fig. 10; Staples, 1997, 1066, fig. 21.7e.

Material Examined. QM-S73270, 2 ♀♀, 1 juv., on filamentous red algae, Point Lookout, 27°26.31′S 153°32.52′E, 10 m, 12.02.2005, A-N.L. QM-S73271, ovigerous ♂, 2 ♀♀, 2 juvs, on algae, Flat Rock, 27°23.5′S 153°33.0′E, 8–15 m, 17.02.2005, A-N.L. QM-S73272, ♀, 1 juv., in hydroids, Shag Rock, north of Point Lookout, North Stradbroke I., 27°24.8′S 153°31.5′E, 8 m, 18.02.2005, M. Preker. NHM.2006.335-337, ovigerous ♂, 2 ♀♀, amongst hydroids, Flat Rock, 27°23.5′S 153°33.0′E, 21 m, 22.02.2005, M. Preker.

Remarks. *Achelia shepherdi* is endemic to Australia, having been recorded from West Australia, Tasmania and Victoria, at depths from 0–50 m. The present records extend its known distribution northwards on the eastern Australian coast to

Queensland. The species is instantly recognisable owing to its bulbous, round proboscis and the exaggerated ventral apophyses on the last four palp articles, giving a serrated appearance to the distal half of the palp. The present material was collected subtidally from amongst hydroid or algal substrata from 8–21 m depth.

Achelia assimilis (Haswell, 1884)

Ammothea assimilis Haswell, 1884: 1026–1027, pl. LV, figs 5–9
Achelia assimilis — Stock, 1954, 97–100, figs 45–46; Arango, 2003, 2728–2730, fig. 2 (literature).

Material Examined. QM-S73273, ♂, ♀, 1 juv., in sponge and bryozoan epifauna, Point Lookout, 27°26.31′S 153°32.52E, 10 m, 12.02.2005, A-N.L. QM-S73274, 2 subadults, 1 juv., amongst bryozoans, Amity Point Jetty, 27°23.9′S 153°26.2′E, 5m, 12.02.2005, M. Preker. QM-S73275, 2 subadults, within dead *Phoronis* tube-mat, Point Lookout, 27°26.31′S 153°32.52E, 10 m, 12.02.2005, A-N.L. QM-S73276, ♂, ♀, 3 juvs, amongst hydroids and algae, Flat Rock, 27°23.5′S 153°33.0′E, 8–10 m, 17.02.2005, M. Preker. QM-S73277, ovigerous ♂, on algae (*Melanamansia glomerata*), QM-S73278, 1 subadult, on *Delisia pulchra*, Flat Rock, 27°23.5′S 153°33.0′E, 8–15 m, 17.02.2005, A-N.L. NHM.2006.338–342, ovigerous ♂, ♂, 2 ♀♀, 1 subadult, amongst hydroids, Flat Rock, 27°23.5′S 153°33.0′E, 21 m, 22.02.2005, M. Preker.

MBWS MATERIAL: QM-S85511, ♀, stn 6B; QM-S85510, ♀, stn 6D; QM-S85522, ♀, stn 6E; QM-S85503, ♀, stn 7A; QM-S85508, 2 ♂♂, ♀, stn 7B; QM-S85512, ♂, 2 ♀♀, stn 7E; QM S85513), ♀, stn 8A; QM-S85523, 2 ♀♀, stn 8C; QM S85515, ♀, stn 8D.

Remarks. This species has been recorded previously from Western Australia, New South Wales and Queensland, as well as from East Africa, South America and from New Zealand up to the Philippines (see Arango, 2003 for discussion). Much variation in its morphology has been described, and it is likely to be a species aggregate. The present material was collected subtidally from amongst epizoic or algal substrata at 5 to 21 m depth.

Family EURYCYDIDAE Sars, 1891

Ascorhynchus Sars, 1877

Ascorhynchus aff. *insularum* Clark, 1971
(Fig. 1)

Ascorhynchus insularum Clark, 1971, 335–336, fig. 2A–L.

Material Examined. QM-S73279, subadult, amongst *Halophila decipiens* on slightly anoxic sand, NE of Chain Banks, 27°24.58′S 153°21.75′E, 7.7–8.5 m, 35‰, 29.4°C, spanner crab dredge, RNB.
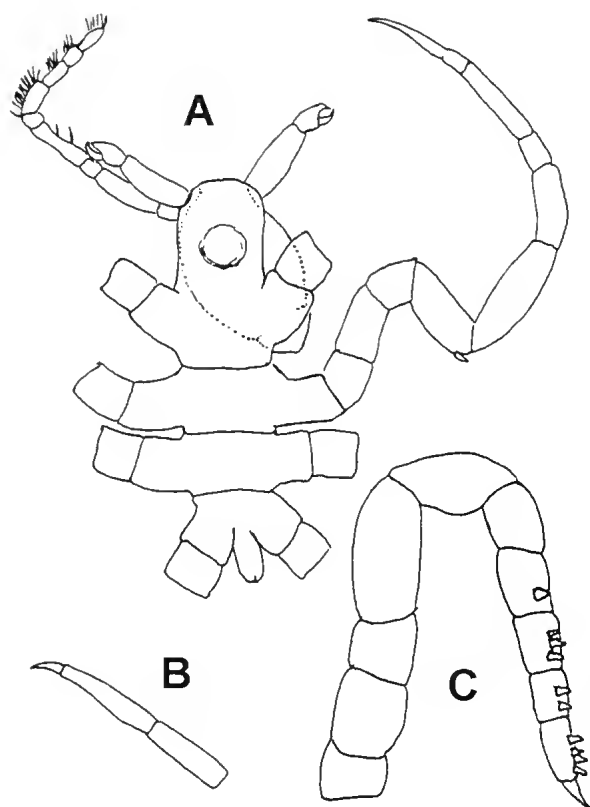
FIG. 1. *Ascorhynchus* aff. *insularum* Clark, 1971, Moreton Bay subadult: A, trunk and second right leg, dorsal; B, detail of distal articles of first right leg; C, left oviger. Scale bar = 0.6 mm for A, B, 0.3 mm for C.

Description. Tiny, trunk length 1.25 mm; trunk (Fig. 1A) fully segmented, glabrous; cephalon half length of trunk, dome-like ocular tubercle in anterior half. No dorsal tubercles on trunk midline, lateral processes or cephalon.

Proboscis fusiform, widest centrally, with slight distal constriction. Chelifore scape of one article; chelae chelate. Palp of ten articles, third and fifth articles (P3 and P5) subequal, longest; P6 half length of P7; P7 to P10 subequal, with ventral setae, restricted to distal half on last three articles. Oviger (Fig. 1C) compact, probably immature; fourth article (O4) longest; compound spines on distal; four articles (1:3:3:5); terminal claw half length of O10, simple.

Second leg (Fig. 1A) almost naked, femur with short, stout dorsodistal spine; tarsus one third as long as propodus; main claw slightly longer than propodus. First leg with reduced main

claw, one-quarter as long as propodus; tarsus not apparent (Fig. 1B).

Remarks. this specimen is a subadult, with fully segmented trunk and all articles present in legs, palps and ovigers; the chelae are still chelate, but compound and terminal spines are present on the oviger. At this stage, most gross adult features of morphology are expressed.

The only described species of *Ascorhynchus* with a tarsus much shorter than half the length of the propodus (brevitarsal), a single-articled chelifore scape, and no dorsal trunk, lateral process or cephalon tubercles are *A. arenicola* (Dohrn, 1881) known only from the Mediterranean near Naples; *A. mariae* Turpaeva, 1971, known only from the Kurile-Kamchatka Trench, NW Pacific, at depths greater than 3000 m; and *A. insularum*, recorded from the littoral zone of the Snares Islands, near New Zealand (Clark, 1971).

In the morphology of the cephalon and of the proboscis, the proximity of the lateral processes, and in particular the proportions of the palp articles, this specimen appears closest to an early subadult of the small species *A. insularum* (trunk length of holotype 3.1 mm). However, the lack of spines and setae on the trunk and legs, other than the short, stout dorsodistal spine on the femur, the lack of a swollen ventral extension of the cephalon at the attachment of the ovigers, and the proportions of the leg articles are inconsistent with that species. An adult specimen is needed for confirmation.

Ascorhynchus longicollis (Haswell, 1885)

A. longicollis Flynn, 1919, 81–83, Pl. XXI, figs 16–17.

Material examined. QM-S85521, ovig. ♂, MBWS stn 5E; QM-S85501, ♀, MBWS stn 10B; QM-S85502, ♀?, MBWS stn 13B.

Remarks. This South Australian species has rarely been recorded (Haswell 1885; Clark 1963). It is distributed from South Australia to Port Jackson (type-locality) and around Tasmania, on sandy bottoms, and to depths of 6 m (Staples 1997). Of the other two *Ascorhynchus* species of South Australia (Staples 1997), *A. compactum* Clark, 1963 is, as its name suggests, compact, with a short neck, and the tarsus is only 0.2 times as long as the propodus (brevitarsal); *A. longicollis* and *A. minutus* Hoek, 1881 are longitarsal species with a long neck, but the latter species has pronounced

mid-dorsal trunk tubercles and comparatively long dorsodistal tubercles on the lateral processes (all minimal or absent in *A. longicollis*), while its ocular tubercle lies halfway between the oviger insertion and the anterior margin of the cephalon, while in *A. longicollis* it is situated above the anterior edge of the oviger insertion.

Family ENDEIDAE Norman, 1908

Endeis Philippi, 1843

Endeis flaccida Calman, 1923

Endeis flaccida Calman, 1923: 295–297, fig. 17; Arango, 2003, 2759–2761, fig. 14 (literature)

Material Examined. NHM.2006.343, ♀, in *Zostera* with *Halophila ovalis* outside Amity Point sand bar, 27°24.3′S, 153°26.15′E, 0 m, 35.5‰, 85% sand, 15% silt- clay, 14.02.2005, RNB. QM-S73280, ♂, 1 juv., amongst hydroids at Shag Rock, north of Point Lookout, North Stradbroke I., 27°24.8′S 153°31.5′E, 8 m, 18.02.2005, M. Preker.

Remarks. *Endeis flaccida* has been recorded from a disjunct distribution, incorporating the Indo-West Pacific and the Caribbean, from depths between 0 and 97m. Arango (2003) was the first to record the species from Australia, amongst *Cladophora prolifera* and bryozoan/ hydroid turf on the Great Barrier Reef, at 0–2 m depth. The species is characterised by its having blind diverticula (caecae) on the gut within the legs.

Family CALLIPALLENIDAE Hilton 1942

Propallene Schimkewitsch, 1909

Propallene ardua Stock, 1975

(Fig. 2)

Propallene ardua Stock, 1975, 92–93, figs 27–41.

Material Examined. QM-S73281, ovig. ♂, clean medium sand, East of Moreton I., 27°18.19′S 153°27.56′E, 20.6 m, 22.02.2005, 0.1m² long-arm van Veen grab, RNB. QM-S73282, subadult ♀, on *Sertularella diaphana* with ectozoic *Hebella* sp., Amity Point, 27°23.9′S 153°26.2′E, 5–10 m, 14.02.2005, A-N.L.

Remarks. Stock (1975) described *Propallene ardua* from material collected in shallow waters off Tanzania, while admitting the similarity between this species, the type-species *P. longiceps* (Böhm, 1879) from Japan, and the south-east Asian species *P. kempi* (Calman, 1923). Close examination of the Moreton Bay specimens failed to find any significant difference from the description and figures of Stock (ibid.); there are nine cement-gland tubes on the femur, two stout and distally crenulate heel spines on the slightly curved propodus, and the long setae on the longer leg articles. Observed differences include the shorter palp (Fig. 2B), a smaller, blunt dorsodistal process on oviger article five, opposite the setose apophysis (Fig. 2D), a more compact first coxa, and the absence of the `prominence' at the base of the main claw described and figured in some detail by Stock for the Tanzanian specimens. These differences are not considered indicative of specific distinction, but probably represent population differences. The Moreton Bay specimens are figured herein to facilitate comparison with the East African type description, as well as with other Eastern Australian species. The apparent zoogeographic disparity of this record may reflect an artificial introduction via the intensive shipping at the Port of Brisbane.

Staples (1979) described the three known Australian species of *Propallene*, *P. cyathus* and *P. vagus* from south-eastern Australia (well south of Moreton Bay), and *P. saengeri* from Gladstone, Queensland (north of Moreton Bay). All of the Australian species have a compact trunk, with lateral processes separated by less than their own width. Conversely, *P. ardua* has lateral processes separated by about their own width, and its legs are significantly more hirsute than those other species, making it easily distinguished. Nakamura & Child (1983) discussed the distinctions of *P. longiceps* (Böhm 1879).

The male was carrying eggs and larvae, the latter (Fig. 2F) at a post-protonymphon stage (as appears the norm for callipallenids), 150 μm in length with short, functional chelae and two pairs of walking legs, but no trace of regressed larval legs.

Oropallene Schimkewitsch, 1929
Oropallene minjerriba sp. nov.
(Fig. 3)

Material Examined. QM-S73283, ♀ holotype, in hydroids at Shag Rock, nr Point Lookout, North Stradbroke I., 27°24.8′S 153°31.5′E, 8 m, 18.02.2005, M. Preker.

Description of Female. Trunk (Fig. 3A) compact, glabrous, fully segmented, length (anterior margin of cephalon to tip of fourth lateral process) 1.0 mm. Cephalon attenuate, half as long as total trunk length, with constricted `neck' and flared
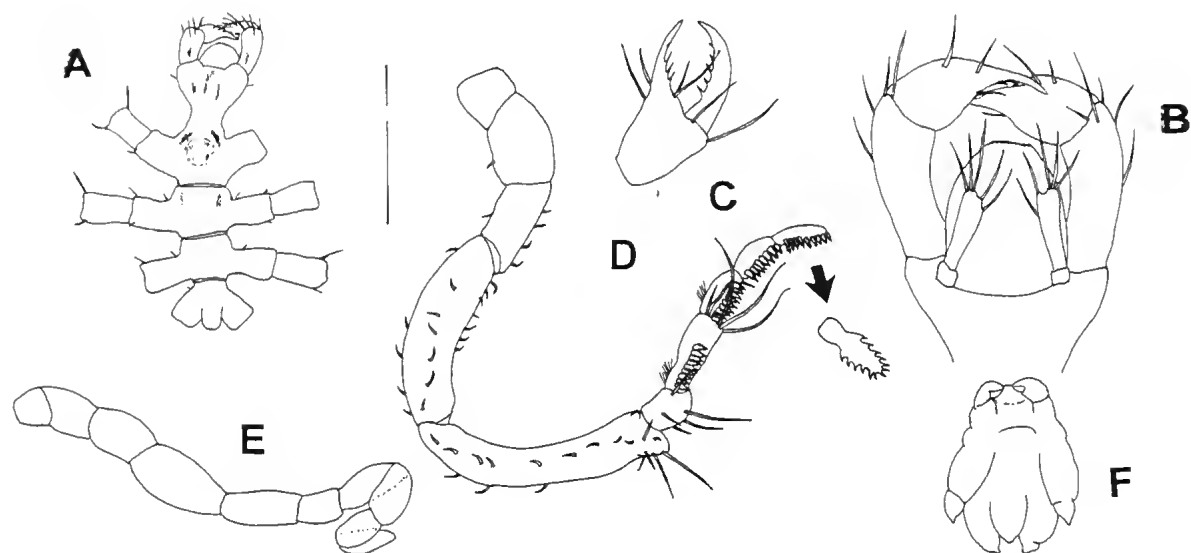
FIG. 2. *Propallene ardua* Stock, 1975, Moreton Bay specimens: **A**, trunk, dorsal; **B**, anterior appendages, ventral; **C**, chela; **D**, left oviger of male, with detail of compound spine; **E**, left oviger of subadult female; **F**, postlarva. Scale bar = 1.0 mm for A, 0.4 mm for B to E, 0.15 mm for F.

to chelifore insertion; single small spines above and just posterolateral to chelifore insertion, similar pair of single small spines antero-ventrally; ocular tubercle a rounded dome at posterior of neck, with four small pigmented eyes and two small dorsolateral tubercles. Chelifore and proboscis attachment at anterior of ceph-alon, oviger attachment below first lateral pro-cesses. Palps absent. Lateral processes separated by less than half of their own diameter, distally with small spines anteriorly and/or posteriorly. Abdomen simple, naked, rising above horizontal, almost reaching distal edge of lateral process of leg 4.

Proboscis short (half length of cephalon), ovoid, with simple lips. Chelifora robust; scape of one article, shorter than proboscis, with sparse distal spines (Fig. 3B); chela (Fig. 3B) typical of genus, fingers straight, fixed finger with two rows of denticulations, moveable finger with six dentic-ulations.

Oviger (Fig. 3C) of ten articles, articles 1 to 3 (O1 to O3) short, subequal, naked; O4 and O5 subequal, longer than any other article, with single (O4) or two (O5) small distal spines; distal five articles subequal in length (O7 just longest); O6 with single simple distal spine; O7; O8, O9 and O10 with three, two, two and three ventral

compound spines respectively, O9 with small simple distal spine, O10 with short, tapering terminal claw bearing minute ventral crenul-ation.

Second leg (Fig. 3D) generally spinose, robust. Coxa 1 shorter than wide, with single anterior and posterior distal spines; coxa 2 1.8 times as long as coxa 1, wider distally, with scattered short spines as figured; coxa 3 half length of coxa 2, with paired ventrodistal spines. Femur relatively stout, twice as long as wide and 4.8 times as long as coxa 3; sparse ring of small spines in proximal half, fewer similar spine sub-distally, paired longer spines distally. Tibia 1 compact, 0.8 times as long as femur, with two mesial bands of small spines, longest dorsal spine on tubercle; distally with sparse short spines and longer dorsal seta. Tibia 2 longest article, 1.3 times as long as tibia 1 and 2.3 times as long as wide, with numerous short spines as figured, longer dorsal spine on tubercle in prox-imal half, and slender dorsal seta in distal half. Tarsus small, subtriangular, with two small and one longer, stout ventral spines. Propodus stout, twice as long as wide, without pronounced heel, with two larger proximal (heel-) spines without denticulations, five sole spines and distal sole seta; scattered small spines and three distal setae
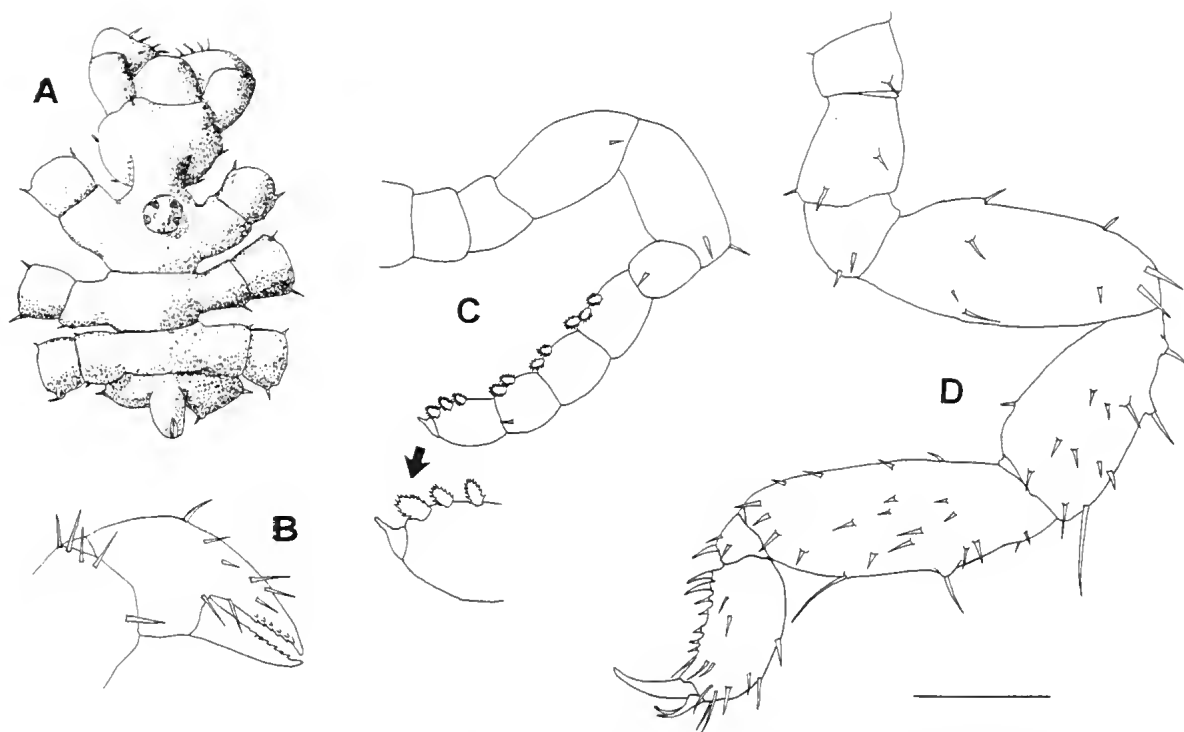
FIG. 3. *Oropallene minjerriba* sp. nov., holotype: **A**, trunk, dorsal (4th trunk segment deflected ventrally); **B**, left chela; **C**, left oviger with detail of spination of distal article; **D**, second left leg. Scale bar = 0.4 mm for A, 0.2 mm for B, C, 0.3 mm for D.

adjacent to main claw insertion. Main claw curved, 0.56 times as long as propodus, auxiliary claws curved, 0.6 times as long as main claw.

MEASUREMENTS OF HOLOTYPE (mm). Trunk length: 1.0; cephalon: 0.5; width across 2nd lateral processes: 0.54. Lengths of oviger articles 1 to 10 respectively: 0.07, 0.07, 0.07, 0.19, 0.18, 0.09, 0.10, 0.09, 0.08 and 0.09. Fourth leg, coxa 1: 0.13; coxa 2: 0.24; coxa 3: 0.12; femur: 0.58; tibia 1: 0.46; tibia 2: 0.60; tarsus: 0.07; propodus: 0.32; main claw: 0.18; auxiliary claw 0.11.

Etymology. `Minjerriba' is an Australian aboriginal name for North Stradbroke Island, off which the holotype was collected (used as a noun in apposition).

Remarks. *Oropallene* is in part characterised by the 4-articled palp found only in the male. The only genus of the Callipallenidae without palps in the male, but with a distal oviger claw and regular denticulations on the chela fingers is *Seguapallene* (Pushkin 1975), species of which do not have a flared crop, but do have a denticulate oviger claw. Of those callipallenid taxa with male palps, the only genera with denticulate oviger spines, a terminal oviger spine and auxiliary claws are *Oropallene* and *Neopallene*.

There is some doubt over the maturity of the single known specimen of *N. antipoda* Stock, 1954 (*vide* Stock 1954: 35): if it is immature, then the mature palp structure may be more than one article, and the species may belong to *Oropallene*. The other two species of *Neopallene*, *N. campanellae* Dohrn, 1881, and *N. azoreusis* Arnaud, 1974, are attenuate, slender-legged forms with an elongate oviger claw (see Arnaud 1974, for discussion). *Oropallene* species have a flared crop, two of these are compact species, with short oviger claws (three if *N. antipoda* proves to be in this genus). The present female, with its short oviger claw, compact body form and distinctively flared crop, is thus attributed to *Oropallene*, and is particularly similar to *O. minor* Clark, 1963 and the type species *O. dimorpha* (Hoek 1898) (and to no other species of any of the three genera mentioned above).

The only Australian species of *Oropallene* described previously is *O. minor*, from Victoria at

39–144 m depth (Clark 1963), to which species *O. minjerriba* sp. nov. bears much gross similarity. *Oropallene minor*, at a trunk length of 1.6 mm, was the smallest described species (hence its specific epithet); *O. minjerriba* is far smaller than *O. minor*, its leg articles are much more compact (tibia 2 six times as long as wide, propodus 3.5 times as long as wide); in addition, the present species has remarkably sparse oviger compound spines (3:2:2:3 plus terminal claw, compared with 7:6:5:5 in female of *O. minor*), the auxiliary claws are only 0.56 times the length of the main claw (two-thirds as long in *O. minor*), and denticulations are present on both chela fingers (only `a few low callosities' on the moveable finger in *O. minor*).

Oropallene minjerriba is by far the most compact species of this genus; should the male be collected, it would be easily recognisable.

Callipallene Flynn, 1929
Callipallene emaciata (Dohrn, 1881)
(Fig. 4)

Pallene emaciata Dohrn, 1881: 193–196: pl. 14, figs 10–21.
Callipallene emaciata — Child: 1979, 41–42 (literature, discussion).
non *Callipallene emaciata* subsp. — Stock, 1954.
non *Callipallene* sp. — Clark, 1963; Bamber, 2005.
non *Callipallene* species indeterminate — Child, 1990.

Material Examined. ♂, amongst hydroids at Shag Rock, nr Point Lookout, North Stradbroke I., 27° 24.8'S 153°31.5'E, 8 m, 18.02.2005, M. Preker (specimen lost). QM-S73284, subadult, on hydroid, Shark Gutter, 27°07.9'S 153°28.7'E, 15 m, 22.02.2005, M. Preker.

Remarks. The distinctions of the species within this genus remain somewhat enigmatic; they are either variable, or the subtlety of distinctions within sibling species are not well understood. The species of *Callipallene* recognised from Australian waters are *C. micracantha* Stock, 1954, *C. novaezealandiae* (Thomson 1884) (both of these were originally described as subspecies of *C. emaciata*), *C. catulus* Lee & Arango, 2003, and probably `*Callipallene* species A' of Child (1975) (*q.v.*). None of these has distal crenulations on the propodal heel spines or the ventral tarsal spines, nor fine denticulation of the auxiliary claws, as shown by the present species (Fig. 4E). In addition, *C. emaciata* sensu stricto has a short `crop' (the region of the cephalon between the ocular tubercle and the chelifore implantation),

unlike *C. micracantha* and *C. novaezealandiae*, and is without the small dorsodistal spines on the lateral-processes, or ventral spine-bearing swelling on the femur characteristic of *C. micracantha* (*vide* Staples 2004). *C. catulus* has no suture between trunk segments 3 and 4 and a quite distinctive, almost globular, trunk morphology (Lee & Arango 2003), while *Callipallene* species A of Child (1975) has very small auxiliary claws (smaller than the propodal sole spines).

Child (1990) recorded what he took to be Stock's (1954) `subspecies' of *C. emaciata* from the Great Barrier Reef at 2 m depth, but also refrained from naming it; Stock's record was from New Zealand.

There are five species of short-necked *Callipallene* which have fine denticulation of the auxiliary claws: Child (1988) discusses the other four, viz. *C. californiensis* (Hall 1913), *C. pectinata* (Calman 1923), *C. panamensis* Child, 1979 and *C. seychellensis* Child, 1988.

It seems highly improbable that all the material attributed to this species from the Mediterranean (type locality is the Gulf of Naples), northwestern Europe (northeastern Atlantic), the Caribbean, the Gulf of Mexico and now eastern Australia represents a single species. However, I can see no evident features which distinguish the present material from Dohrn's species.

Pseudopallene Wilson, 1878
Pseudopallene reflexa (Stock, 1968)

Spasmopallene reflexa Stock, 1968, 40–42, fig. 15.
Pseudopallene reflexa — Staples, 2004, 164–166, fig. 4.

Material Examined. QM-S73285, ovigerous ♂, ♀, subadult, NHM.2006.344–345, larvigerous ♂, 1 subadult in ethanol, on the bryozoan *Orthoscuticella ventricosa* agg, Henderson's Pinnacles, East side of Moreton I., 27°07.901'S 153°28.712'E, 22–26 m, 22.02.2005, A-N. L.

Remarks. The long-standing confusion over the Antipodean representatives of this genus, together with the genera *Spasmopallene* and *Pallenella*, has been recently and competently resolved by Staples (2004), who presented a key to the Australian species of *Pseudopallene*, of which the other two genera are junior synonyms. *Pseudopallene dubia* Clark, 1963, was returned to its original genus, and *Spasmopallene reflexa* and *Pellenella laevis* (Hoek 1881) were moved to *Pseudo-*
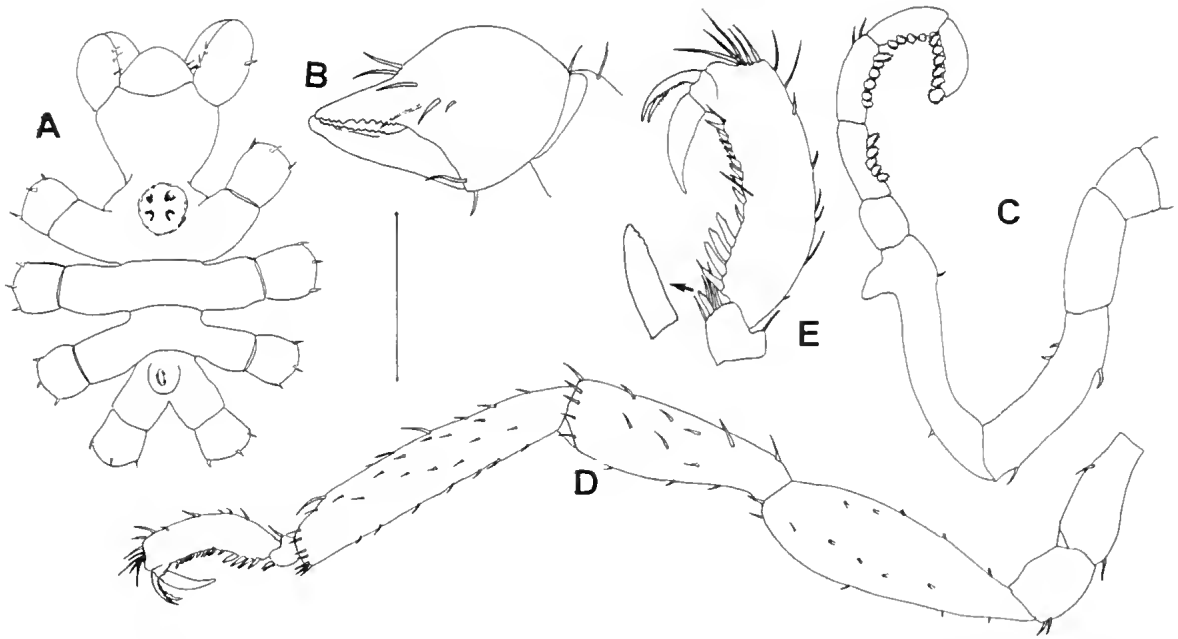
FIG. 4. *Callipallene emaciata* (Dohrn, 1881), Moreton Bay specimen: **A**, trunk, dorsal; **B**, chela; **C**, oviger; **D**, third leg; **E**, distal articles of third leg, with detail of tarsus spine. Scale bar = 0.4 mm for A, D, 0.2 mm for B, C and E.

pallene. Bamber (2005) synonymised *S. clarki* with *P. dubia*.

The present material has the distinct serrated oviger claw of *P. reflexa* as well as the characteristic heel-spine configuration of two basal spines, eight spines in two parallel rows of four each, and one distal spine. The Moreton Bay specimens differ from those described by Staples (*ibid*) from South Australia in that the longer leg articles are without the irregular surface of low swellings; nor are they as compact as those of the holotype (Stock 1968). Staples' material was also collected from one of the four taxa within *Orthoscuticella ventricosa* agg., and, as with the present material, had taken on the exact colouration of the bryozoan.

Family PHOXICHILIDIIDAE Sars, 1891

Anoplodactylus Wilson, 1878

Anoplodactylus cribellatus Calman, 1923

A. cribellatus Calman, 1923: 285–287, fig. 12; Bamber, 1997: 46–49, fig. 2 (synonymy); *A. simplex* Clark, 1963: 50–51, fig. 25.

Material examined. QM-S85526, subadult ♂, MBWS stn 3A; QM-S85509, ovig. ♂, MBWS stn 3B; QM-S85505,

♀, MBWS stn 3C; QM-S85524, ♂, MBWS stn 3E; QM-S85518, ovig. ♂, MBWS stn 4C.

Remarks. Bamber (1997) investigated the three described species of *Anoplodactylus* with more than 10 cement-gland pores per femur in the male, and concluded that the Australian *A. simplex* Clark, 1963 and the Japanese *A. perforatus* Nakamura & Child, 1982, were synonymous with Calman's species, described originally from Indian waters. Previous Australian records are from Townsville, Qld, Botany Bay, NSW, and Esperance, WA, and at depths from 0–30 m. It is readily distinguished from the only other *Anoplodactylus* species recorded in Moreton Bay (*A. tubiferus*, see below), as it has a low, dome-like ocular tubercle (see Arango, 2003, for key to Australian species of *Anoplodactylus*).

Anoplodactylus tubiferus (Haswell, 1885)

Anoplodactylus tubiferus − Staples, 1982: 457, fig. 2 (literature, synonymy); Müller, 1989: 281–282, figs 15–20.

Material examined. QM-S85516, ♀, MBWS stn 1B; QM-S85527, 2 ♂♂, ♀ MBWS stn 1C; QM-S85528, ♀, MBWS stn 1E; QM-S85507, ♀, MBWS stn 2E; QM-S85518, S85520, 2 ♀♀, MBWS stn 3E; QM-S85528, 2 ♂♂, MBWS stn 5B; QM-S85506, ♂, ♀, MBWS stn 5E.

Remarks. This species, with a characteristically tall, slender ocular tubercle, has a wide distribution around the Indo-West Pacific (see Müller 1989), in depths from the subtidal to 135 m. In Australia it has been recorded previously from the Great Barrier Reef, Qld, Victoria, NSW, and WA.

Family NYMPHONIDAE Wilson, 1878

Nymphon Fabricius, 1794

Nymphon molleri Clark, 1963

Nymphon molleri Clark, 1963: 10–12, fig. 6.

Material examined. ♀, MBWS stn 3C (det. C. Arango).

Remarks. This species is only known from Australia — from the Great Barrier Reef, Qld, to South Australia and the Great Australian Bight, at depths of 5–112 m. It has a long neck, chela fingers longer than the palm, a short tarsus and short claws on the propodus.

Nymphon boogoora sp. nov.
(Fig. 5)

Material examined. HOLOTYPE: QM-S85514, ♀, MBWS stn 2D. PARATYPES: QM-S85517, ♀, MBWS stn 2E; QM-S85504, ♀, MBWS stn 5E. OTHER MATERIAL: 1 spec., MBWS stn 4E; 1 spec., MBWS stn 10D (det. C.Arango).

Description of Female. Small nymphonid, holotype trunk length 1.7 mm; trunk (Fig. 5A, B) not compact, glabrous, fully segmented. Cephalon 0.43 times as long as total trunk length, without ornamentation, with appearance of 'crop' but no parallel-sided neck region; dome-like ocular tubercle in centre of cephalon, with four eyes; oviger attachment below anterior margin of first lateral processes. Lateral processes naked, separated by more than their own diameter. Abdomen simple, clavate, almost horizontal, nearly reaching distal edge of coxa 1 of leg 4.

Proboscis (Fig. 5B) barrel-shaped, naked, directed anteroventrally, 0.3 times as long as trunk.

Chelifore scape of one article, slender, two-thirds as long as proboscis; chela (Fig. 5C) slender, fingers twice as long as palm; moveable finger with 16 pointed, curved teeth; fixed finger with 17 blunt, curved teeth.

Palp (Fig. 5D) of 5 articles. First article (P1) short, compact; P2 and P3 elongate, P3 0.8 times as long as P2; P4 just shorter than P5, these two together 0.9 times as long as P3. P4 and P5 densely setose.

Oviger (Fig. 5E, F) of 10 articles, article 5 (O5) longest; articulations between O2 and O3 and between O4 and O5 anaxial; O7 to 10 setose, with compound spines in the formula 8:5:4:5 (proximal spine on O7 without lateral denticulations); terminal claw with five ventral teeth.

Third leg (Fig. 5G) elongate, slender. Coxa 1 compact, naked; coxa 2 more than three-times as long as coxa 1, with single ventrodistal gonadopore; coxa 3 0.4 times as long as coxa 2; femur 1.6 times as long as coxa 2, finely setose, dorsodistally with longer seta. Tibia 1 1.3 times as long as femur, slender, sparsely setose; tibia 2 longest article, 1.1 times as long as tibia 2, slender, with robust ventrodistal curved spine. Tarsus slender, elongate, with short ventral setae, 0.8 times as long as propodus. Propodus slender, elongate, with short ventral setae, without heel; main claw half length of propodus; auxiliary claws conspicuous, slender, 0.8 times length of main claw.

Male unknown.

MEASUREMENTS OF HOLOTYPE FEMALE (mm). Trunk length: 1.70; cephalon: 0.73; width across 2nd lateral processes: 0.94; abdomen length: 0.27; proboscis length: 0.52. Lengths of palp articles 1 to 5 respectively: 0.04; 0.44; 0.36; 0.14; 0.16. Lengths of oviger articles 1 to 10 respectively: 0.09; 0.20; 0.20; 0.57; 0.63; 0.34; 0.21; 0.16; 0.14; 0.14. Third leg, coxa 1: 0.28; coxa 2: 1.00; coxa 3: 0.37; femur: 1.66; tibia 1: 2.11; tibia 2: 2.34; tarsus: 0.49; propodus: 0.63; main claw: 0.31; auxiliary claw: 0.25.

Etymology. *Boogoora* is an Australian aboriginal name for Moreton Bay.

Remarks. Eleven shallow-water (<200 m) *Nymphon* species have been recorded from Australia. Clark (1963) listed six species, *N. aequidigitatum* Haswell, 1884, *N. immane* Stock, 1954, *N. singulare* Stock, 1954, *N. molleri* (see above), *N. novaehollandiae* Clark, 1963, and *N. bunyipi* Clark, 1963. Subsequently Stock (1973a) described *N. comirostrum* and *N. dubitabile* as new species from south-eastern Australia; Child (1975) described two new species from Western Australia, subsequently synonymised to one species (*N. rottnesti* Child, 1975) by Bamber (2005); Child (1990) described *N. draconis* from the Great Barrier Reef, and Arango (2003) recorded *N. micronesicum* Child, 1982, also on the Great Barrier Reef.

The present species, with no lateral process tubercles, lateral processes separated by more
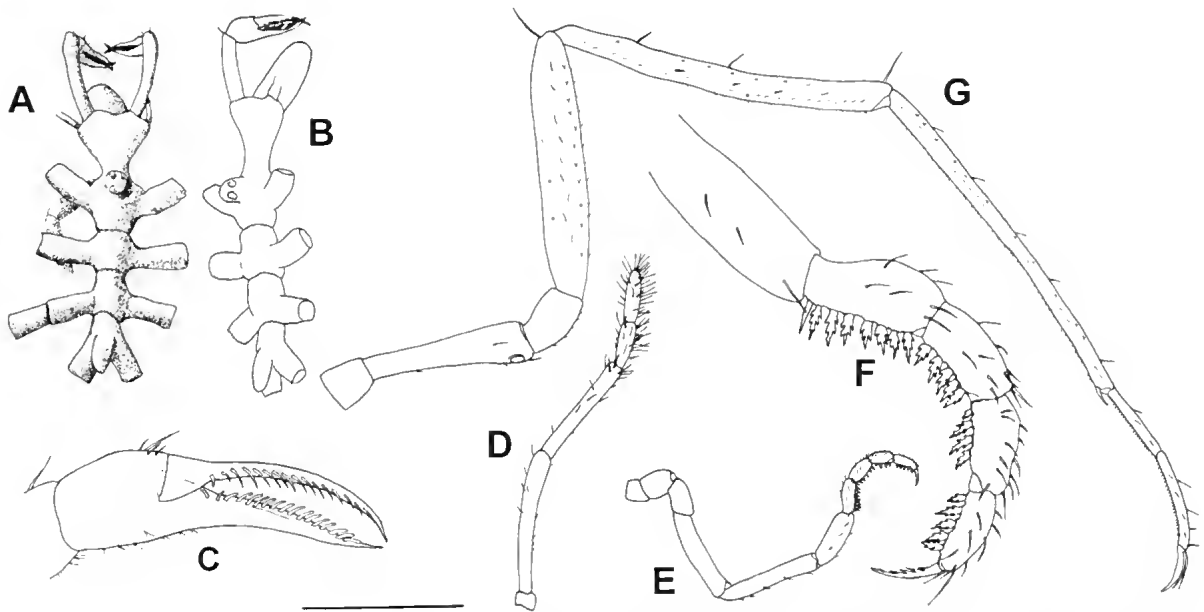
FIG. 5. *Nymphon boogoora* sp. nov., holotype: **A**, trunk, dorsal; **B**, trunk, dorsolateral; **C**, right chela; **D**, right palp; **E**, right oviger; **F**, detail of distal oviger articles; **G**, third right leg. Scale bar = 1 mm for A, B, E and G, 0.25 mm for C, F, 0.5 mm for D.

than their own diameter, auxiliary claws shorter than the main claw, and a slender tarsus more than half as long as the propodus, both with simple ventral setation, is similar only to *N. rottnesti* and *N. molleri*. Unlike *N. boogoora* sp. nov., both of those species have a distinct, narrow, parallel-sided neck region to the cephalon between the ocular tubercle and the flaring of the crop to the point of insertion of palps and chelifore; in addition, they have more compound spines on the oviger strigilis, and the fifth palp article is shorter than the fourth (just longer in the present species). The curved ventrodistal spine on tibia 2 in *N. boogoora* is not found in the other species.

The only shallow-water species from New Zealand is *N. maoriana* Clark, 1958, a larger species with a similar trunk conformation, but with quite different morphology of the chela and palp, and auxiliary claws less than half the length of the main claw (*inter alia*).

Staples (1997) gave a key to the six *Nymphon* species of southern Australia, which is expanded below to cover the twelve species now recorded from Australian waters of <200 m depth.

Key to Australian species of *Nymphon* (<200 m depth)

1. Lateral processes with dorsodistal tubercles; cephalon over chelifore bases and coxae with or without tubercles. 10
 — Lateral processes, cephalon over chelifore bases and coxae without dorsodistal tubercles. 2

2. Oviger attachment distinctly separated from and anterior of first lateral processes. . . . 3
 — Oviger attachment in contact with first lateral processes. 6

3. Auxiliary claws as long as or longer than main claw (*N. aequidigitatus*-group); fifth palp article more than twice as long as fourth; tarsus about half or less as long as propodus; proboscis swollen at midlength. 4
 — Auxiliary claws less than half length of main claw; fifth palp article shorter than fourth; tarsus three-quarters as long as propodus; proboscis cylindrical. . . . . *N. bunyipi*

4. Tarsus half as long as propodus; main and auxiliary claws without denticulation; palp articles 3 and 5 subequal in length. 5
 — Tarsus much less than half length of propodus; main and auxiliary claws with proximo-

ventral denticulations; palp article 3 much shorter than article 5. . . . *N. micronesicum*

5. Fifth palp article three times as long as fourth; chela fingers more than half length of palm; setae on distal palp and oviger articles shorter than article width. . . . . .
. . . . *N. aequidigitatum*

— Fifth palp article about twice as long as fourth; chela palm bulbous, 1.5 times as long as wide, fingers half length of palm; setae on distal palp and oviger articles longer than article width. . . . . *N. draconis*

6. Lateral processes separated by more than their own diameter; proboscis cylindrical. 7

— Lateral processes separated by about half their own diameter; proboscis conical; cephalon compact, neck broad. . *N. conirostrum*

7. Tarsus longer than propodus, propodus with long proximal sole spines. . . . *N. dubitabile*

— Tarsus 0.8 times or less as long as propodus, propodus with no long sole spines. 8

8. Cephalon with distinct, slender, parallel-sided neck region; palp article 4 longer than article 5; distal three oviger articles with at least 8 compound spines. 9

— Cephalon without parallel-sided neck region; palp article 4 just shorter than article 5; distal three oviger articles with less than 6 compound spines. . . . . *N. boogoora*

9. Cephalon neck narrower than proboscis and half length of cephalon; terminal oviger claw distally rounded and crenulate; chela fingers 1.5 times as long as palm (eastern and Southeastern Australia). . . . *N. molleri*

— Cephalon neck one-third or less length of cephalon; terminal oviger claw distally pointed; chela fingers twice as long as palm (Western Australia). . . . . . . *N. rottnesti*

10. Coxa 1 with conspicuous dorsodistal tubercles; no tubercles over chelifore bases. . . . . .
. . . . *N. novaehollandiae*

— Anterior cephalon at chelifore insertion with low, rounded single tubercles; coxae without dorsodistal tubercles. 11

11. Lateral processes separated by about their own diameter; palp articles 4 and 5 subequal in length, together as long as third article; twice as many and finer teeth on fixed finger of chela than on moveable finger (teeth dimorphic). . . . . *N. immane*

— Lateral processes hardly separated from each other; palp article 5 much shorter than article 4, these two together longer than article 3; similar teeth on both chela fingers (monomorphic). . . . . *N. singulare*

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Tanaidaceans (Crustacea: Peracarida: Tanaidacea) from Moreton Bay, Queensland

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ABSTRACT

Sampling of the littoral and sublittoral benthos around Moreton Bay, Queensland, Australia, undertaken in February 2005, revealed, *inter alia*, 1175 specimens of tanaidacean, representing 29 species in 20 genera. Four of these species in the Parapseudidae, including three new species and one new genus, have been treated elsewhere. All of the material is discussed herein, including 17 further new species, comprising one kalliapseudid, one synapseudid, and one pagurapseudid, one tanaid, two anarthrurids, one typhlotanaid, two paratanaids and seven leptocheliids, and three further new genera, one in the Anarthruridae, one in the Typhlotanaidae and one in the Leptocheliidae. Range extensions of a number of species are reported, including taxa recorded previously from Western Australia, New South Wales and New Caledonia. *Heterotanais crassicornis* is transferred to *Konarus*. The diversity and niche specificity of these taxa in the Moreton Bay region is discussed. Existing samples held in the Queensland Museum were also examined, and contributed a further new species as well as additional taxa, and further records of the new taxa found in 2005. A complete listing is given of the known Australian species of Tanaidacea (not including those from Subantarctic waters). ❏ *Crustacea, Tanaidacea, Apseudomorpha, Tanaidomorpha, Queensland, Australia, Antiplotanais, Bathytanais, Bunakenia, Curtipleon, Gollumudes, Kalliapseudes, Konarus, Leptochelia, Longiflagrum, Pagurotanais, Pakistanapseudes, Paratanais, Pseudoleptochelia, Catenarius, Remexudes, Sinelobus, Tanaopsis, Tangalooma, Teleotanais, Whiteleggia, Zeuxo.*

Sampling of the littoral and sublittoral benthos around Moreton Bay, Queensland, was undertaken in February 2005 in order to characterise the smaller marine arthropod fauna of this region, including tanaidaceans. In the event, 1175 specimens of tanaidacean were collected, representing 29 species in 20 genera, of which 20 species and 4 genera were new to science. Range extensions of a number of known species were discovered, including taxa recorded previously from Western Australia, New South Wales and New Caledonia. Four of these species, including three new species and one new genus in the Parapseudidae, have been treated elsewhere (Błażewicz--Paszkowycz & Bamber, 2007a). Existing samples held in the Queensland Museum were also examined, and included further material of the

new taxa found in 2005, and an additional new species of the Tanaidae. All this material is described or discussed below.

Listings of tanaidaceans from all Australian waters were given by Poore (2002, 2005). The previous records of Tanaidacea from Australia (not including Antarctica) were reviewed by Bamber (2005), who listed 28 known species, and added two new genera and 24 new species from Western Australia. To that list should be added *Bathytanais bathybrotes* (Beddard 1886), as some of Beddard's material came from Port Jackson, New South Wales. While the early records are sparse, studies since the end of the 1990s (Larsen 1999, 2000, 2001; Larsen & Heard 2001; Larsen & Hansknecht 2002; Guțu & Heard

2002; Bamber 2005; Guţu, 2006; Drumm & Heard 2006b; Błażewicz-Paszkowycz & Bamber, 2007a, b; Edgar, 2008) have demonstrated an unusually high density and diversity of tanaidaceans in Australian waters; most surprisingly, Larsen & Hansknecht (2004) described as new *Pseudo-halmyrapseudes aquadulcis* from a freshwater spring in Northern Territory. Of particular relevance here, Boesch (1973) recorded three new species from Moreton Bay. Also, Guţu (2006) described 13 new species of apseudomorph tanaidacean from Australian waters; six of these were collected from Moreton Bay in 1976. Four of these six were not collected in 2005, including, perhaps surprisingly, the apseudid *Muramurina splendida* (Guţu, 2006) (Apseudinae), which was recorded as an estimated 1500 specimens from Middle Banks, to the west of Moreton Island, in 1976. Most recently, Edgar (2008) described 12 new species of the family Tanaidae from Australian waters.

A complete listing of the 113 known Australian species of Tanaidacea (not including those from Subantarctic waters), including the species described below, is given as Appendix 1.

METHODS

Collecting methods were by hand (diving) and by various sampling gears, notably long-arm and standard 0.1 m² van Veen grabs and a spanner-crab dredge. Other sampling was opportunistic and non-quantitative. Sample depths ranged from the littoral zone to 41.3 m. Position fixing was by GPS. All specimens were collected under Queensland Marine Parks Permit No. QS2005/CVL1057.

Specimens were sorted live, colour noted, then fixed in 100% ethanol or 75% methanol. Drawings were all done using a camera lucida. Measurements are axial, dorsally on the trunk and laterally on the appendages. Voucher and type-material has been lodged in the collections of The Queensland Museum (QM) and The Natural History Museum, London (NHM).

Station details for grab samples collected by Peter Davie from his intensive survey of Moreton Bay south of Peel Island during the 2005 workshop are given in Table 1; these samples are referred to in the text as 'MBWS Stn #'. Abbreviations for collectors listed: Roger Bamber (RNB) ; Peter Davie (PJFD); Anne-Nina Lörz (A-NL).

The higher taxonomy of the suborder Tanaidomorpha is largely based on Sieg (1980) for the Tanaoidea and on Guţu & Sieg (1999) for the Paratanaoidea. Recently Larsen & Wilson (2002) produced a re-interpretation of the higher taxonomy of the Paratanaoidea derived from cladistic analysis; while potentially a positive step in sorting out the complexity of the superfamily, it left a large number of genera unclassified (*incertae sedis*). Until the remaining taxa are brought into the higher taxonomy, and the somewhat arbitrary divisions based on cluster analysis are given sound taxonomic justification, this analysis must be regarded as only preliminary.

Morphological terminology follows Bamber & Sheader (2005). Serially repetitive body-parts, such as the subdivisions of the antennal flagella and of the uropod rami are segments, while those with independent musculature (such as the parts of the pereopods) are articles. The term 'spines' is used in the traditional (and etymologically correct) sense of rigid 'thorn-like' structures (avoiding the contextual oxymoron 'spiniform setae' *sensu* Watling 1989) to distinguish them from the flexible 'hair-like' setae; non-articulating spine-shaped extensions of the cuticle are mainly considered to be apophyses.

Table 1. Station details for the MBWS survey of February 2005, south of Peel Island, Moreton Bay, Queensland.

Stn	Latitude	Longitude	Depth (m)	Date
1	27° 31.25'	153° 22.00'	5.7	17/02/2005
2	27° 31.25'	153° 21.85'	5.8	17/02/2005
3	27° 31.25'	153° 21.65'	5.6	18/02/2005
4	27° 31.53'	153° 21.44'	5.1	20/02/2005
5	27° 31.53'	153° 21.70'	5.7	20/02/2005
6	27° 31.55'	153° 20.80'	7.7	18/02/2005
7	27° 31.48'	153° 20.72'	8.2	18/02/2005
8	27° 31.48'	153° 20.48'	8.4	18/02/2005
10	27° 31.68'	153° 20.54'	7.6	18/02/2005
13	27° 31.98'	153° 20.62'	6.2	20/02/2005

SYSTEMATICS

Suborder APSEUDOMORPHA Sieg, 1980
Superfamily APSEUDOIDEA Leach 1814
Family APSEUDIDAE Leach, 1814

Bunakenia Guţu, 1995

Bunakenia (Extensibasella) anomala
Guţu, 2006
(Fig. 1)

Bunakenia (Extensibasella) anomala, Guţu, 2006: 105–109, figs 130–142.

Material Examined. QM-W28072, subadult ♂, ♀ without oostegites, dissected, topotypes, medium muddy sand with shell, NE of Banana Bank, Moreton Bay, 27°32.53′S, 153°20.99′E, 4.2 m, 35‰, 28.8°C, 11.02.2005, van Veen grab, RNB. QM-W28452, 5 ♀♀ (3 brooding), Stn. 2; QM-W28453, brooding ♀, MBWS Stn. 3; both van Veen grab, PJFD.

Supplementary Description. Pleotelson rectangular, elongate, just less than half length of pleon, 1.3 times as long as wide. Labrum rounded, simple, naked. Maxilla moveable endite virtually fused, fixed endite with two bifurcate and one bilaterally denticulate distal spines, other spines and setae simple, rostral row of 15 setae. Maxilliped first palp article with longer, inner distal seta and shorter outer seta; second palp article with inner margin bearing about 13 setae largely in two rows, and long outer distal seta reaching tip of fourth article; third palp article with six recurved setae on blunt innerdistal apophysis; fourth palp article with five longer recurved setae and one shorter, straight distal seta.

Cheliped of subadult male (Fig. 1A) slender, basis twice as long as wide, ventrally with stout central spine and paired subdistal setae; three-articled exopodite present, distal article with four plumose setae. Merus subrectangular, with single inner and four ventral subdistal setae; carpus slender, 3.7 times as long as wide, not as compact as that of adult male; chela as that of female.

Pereopod 1 (Fig. 1B) as type. Pereopod 2 (Fig. 1C) basis 2.5 times as long as wide, with single fine elongate dorsal and ventral proximal setae and ventrodistal seta longer than basis width; ischium longer than wide with two ventrodistal setae; merus shorter than carpus, with simple ventral and distal setae, one short and one

longer ventral slender blunt spines and dorso-distal slender blunt spine longer than merus; carpus dorsally with four distal setae and subdistal spine, and single ventrodistal blunt spine, smaller adjacent blunt spine, and smaller proximal ventral spine; propodus slender, sparsely setose, with three ventral spines becoming progressively longer distally, single dorsodistal spine and two smaller spines on posterior face; dactylus slender with small dorsal seta, unguis distinct. Pereopod 3 (Fig. 1D) similar to pereopod 2, but basis three times as long as wide with two midventral setae longer than basis width, ischium with small dorso-distal spine and single seta, carpus with single ventrodistal spine but no dorsal spine, propodus with two dorsodistal spines.

Pereopod 4 (Fig. 1E) basis stouter, 2.3 times as long as wide, with short ventral setae apart from long ventrodistal seta; ischium with single short dorsal and longer ventrodistal setae; merus with two ventral blunt spines; carpus nearly twice as long as merus, ventrally with two proximal spines, distally with row of five slender, blunt spines increasing in length from ventral to dorsal margins; propodus with dorso-distal group of four spines and one seta, most longer than dactylus; dactylus plus unguis shorter than propodus. Pereopod 5 (Fig. 1F) similar to pereopod 4, carpus proportionately longer and with spines arranged ventrally, propodus with distal, subdistal and proximal ventral spines, dactylus plus unguis longer than propodus. Pereopod 6 (Fig. 1G) with two long plumose setae dorsally on merus, four on carpus; propodus ventral margin with row of some 13 small leaf-like spines not extending to proximal margin, dorsodistal group of two blunt spines and single seta, dactylus plus unguis longer than propodus.

Remarks. Guţu (2006) described this species from five females and two males collected from Middle Banks, Moreton Bay in Autumn 1976. The present male is much smaller than the male holotype (2.2 mm compared with 4 mm), and the cheliped has not developed the full dimorphic structure shown by the holotype; a penial tubercle is present midventrally on pereonite 6.

The present material has allowed the foregoing additional description to complement that
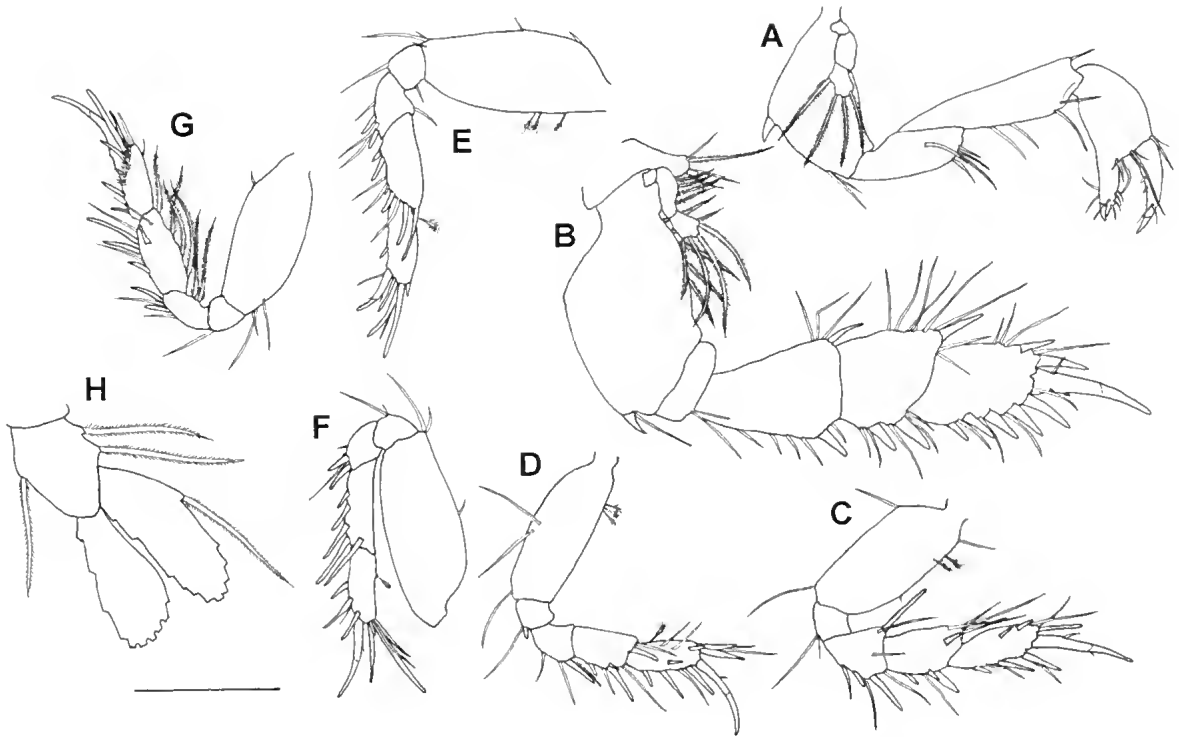
FIG. 1. *Bunakenia (Extensibasella) anomala*, subadult male, **A**, cheliped; **B–G**, pereopods 1–6 respectively; **H**, second pleopod (most setae omitted). Scale bar = 0.2 mm for A–G; 0.1 mm for H.

of Guţu (*loc. cit.*). In particular, he described the distal article of the mandibular palp as having three long and two very small distal setae; in fact the paired small setae are denticulate spines. In addition, pereopods 2–6 were not originally described.

The diet, judging from the gut contents of fine sediment particles, was detritus.

Gollumudes Bamber, 2000

Gollumudes larakia (Edgar, 1997)

Apseudes larakia Edgar, 1997: 279–286, figs 1–3.
Gollumudes larakia — Guţu, 2001: 85–86, 92 (synonymy). Błażewicz-Paszkowycz & Bamber, 2007b: 127–131.

Material Examined. QM-W28073, ♂ (dissected), manca, coarse sand with pebbles and gorgonians, southeast of Bribie I., 27°02.46'S, 153°11.49'E, 8.3 m, 35‰, 28.8°C, 23.02. 2005, van Veen grab, RNB.

Remarks. Guţu (2001) corrected the type-description of this species, pointing out that, contrary to that description, both cheliped and pereopod 1 have an exopodite. Edgar (1997)

recorded large numbers of this species in shallow water (1–8 m depth) around Darwin, Northern Australia, in association with algae and coral rubble. Guţu (2006) recorded five females from Middle Banks, Moreton Bay, collected in 1976, and Błażewicz-Paszkowycz & Bamber (2007b) recorded numerous specimens from the Bass Strait, and to depths of over 60 m, extending its distribution much further south. The present Moreton Bay male differs slightly from the type in having only five articles in the main flagellum of the antennule.

Family Whiteleggiidae Guţu, 1972

Whiteleggia Lang, 1970

Whiteleggia stephensoni Boesch, 1973

Whiteleggia stephensoni Boesch, 1973: 181–187, figs 7–9.
Whiteleggia incerta Guţu, 2006: 297–301, figs 590–600 (new synonymy).

Material Examined. QM-W28074, 26 mature ♂♂, 17 subadult ♂♂, 56 ♀♀ (9 brooding), 12 juvs, 3 further

♂♂, 3 further brooding ♀♀, muddy sand with spatangoids, Moreton Bay, 27°20.91'S, 153°19.96'E, 16.6 m, 33l, 29.1°C, 10 .02.2005, van Veen grab, RNB. NHM 2006.1520–1529, in ethanol, 3 mature ♂♂, subadult ♂, 13 ♀♀ (4 brooding), 5 juvs, sandy mud, Moreton Bay, 27°22.72'S, 153°19.43'E, 15 m, 35‰, 29.4°C, 10.02.2005, van Veen grab, RNB. QM-W28075, topotypic ♂, mud with shell breccia, north of Peel I., Moreton Bay, 27°29.39'S, 153°19.92'E, 8.7 m, 35‰, 29.2°C, 11.02.2005, van Veen grab, RNB. QM-W28076, ♀, sandy mud with seagrass, Banana Bank, Moreton Bay, 27°32.46'S, 153120.74'E, 3.1 m, 33‰, 28°C, 17.02.2005, van Veen grab, RNB. QM-W28454, 24 ♀♀, 11 ♂♂, MBWS Stn. 2; QM-W28455, 4 ♀♀, 3 ♂♂, subadult, MBWS Stn. 3; QM-W28456, ♂, ♀, MBWS Stn. 4; QM-W28457, 10 ♀♀ (1 brooding), 9 ♂♂, MBWS Stn. 5; QM-W28458, 5 ♀♀, ♂, MBWS Stn. 6; QM-W28459, 2 ♂♂, MBWS Stn. 7; QM-W28460, 4 ♀♀, 3 ♂♂, MBWS Stn. 8; QM-W28461, ♂, MBWS Stn. 9; QM-W28462, ♂, MBWS Stn. 13; all van Veen grab, PJFD.

Remarks. The type locality for *Whiteleggia stephensoni* is near Peel Island, Moreton Bay, at 5–6 m depth, in silts and fine sands. It is reassuring to find the species still present, and in large numbers. The present material, all from inside Moreton Bay and from similar substrata as the type-collection, extends the depth range to 3–17 m. Guṭu (2006) described a new species, *W. incerta*, from the mouth of the Brisbane River (coll. March, 1976), based on a single female without oostegites; its morphology is quite within the variation of the present material, and compatible with its being an immature *W. stephensoni*.

Family Kalliapseudidae Lang, 1956

Subfamily Kalliapseudinae Lang, 1956

Transkalliapseudes Drumm & Heard, 2006

Transkalliapseudes banana sp. nov.

(Figs 2–4)

Material Examined. HOLOTYPE: QM-W28077, ♂, medium muddy sand with shell, NE of Banana Bank, Moreton Bay, 27°32.53'S, 153°20.99'E, 4.2 m, 35‰, 28.8°C, 11.02.2005. PARATYPES: QM-W28078, brooding ♀ (head missing), 2 mancae, ♂ (dissected), sandy mud with some seagrass, NE of Banana Bank, Moreton Bay, 27°32.46'S, 153°20.74'E, 3.1 m, 33‰, 28°C, 17.02. 2005, both van Veen grab, RNB. QM-W28169, ♀ allotype, QM-W28170, ♂, MBWS Stn. 10, van Veen grab, PJFD.

OTHER MATERIAL. QM-W28463, 2 ♂♂ MBWS Stn. 11; QM-W28464, ♂ MBWS Stn. 12; all van Veen grab, PJFD.

Description of Male. Body (Fig. 2A) dorsoventrally flattened, small, holotype 4 mm long, 5 times as long as wide, unpigmented. Cephalothorax subrectangular, just wider than long, with pronounced indented rostrum; eyelobes clearly distinguished, eyes absent. Six free pereonites; pereonites 1–3 subequal, about one third as long as cephalothorax; pereonites 4 and 5 subequal, longer, 1.3 times as long as pereonite 2, pereonite 6 shortest (pereonites respectively 3.3, 3.1, 3.0, 2.1, 2.4 and 3.3 times as wide as long). Pleon of five free subequal pleonites bearing pleopods, each pleonite with eight posterolateral setae, otherwise naked. Pleotelson pentagonal, stepped at point of attachment of uropods, longer than last three pleonites together, 1.1 times as wide as long; marginally with three lateral setae and five posterior setae on each side. Penial tubercle present midventrally on pereonite 6, small pointed hyposphenium present midventrally on pleonite 1.

Antennule (Fig. 2B) proximal peduncle article 3.8 times as long as wide, with inner and outer lateral setae longer in the distal half; second article 1.5 times as long as wide, about one quarter length of first, with 2 outer and 1 inner laterodistal setae longer than article length, two outer and 12 inner distal plumose sensory setae; third article half length of second, 1.3 times as long as wide with inner and outer distal setae longer than article length; fourth peduncle article two-thirds as long as third. Main flagellum of eight segments with sparse setation, segments 1–7 with 3, 3, 1, 1, 1, 0 and 1 aesthetascs respectively, distal segment with four distal setae; accessory flagellum of four segments, distal segment with three longer and one tiny distal setae.

Antenna (Fig. 2C) with inner process on proximal peduncle article bearing three plumose distal setae, inner margin of process denticulate. Second article with outer extension surpassing distal margin of third peduncle article, elongate squama with two outer marginal and two distal simple setae, inner margin denticulate. Third peduncle article short, probably representing fusion of third and fourth articles, with two plumose inner setae. Fourth article 3.7 times as long as wide, with inner marginal row of six shorter plumose filtering setae, and midventral row of 20 longer plumose filtering setae,
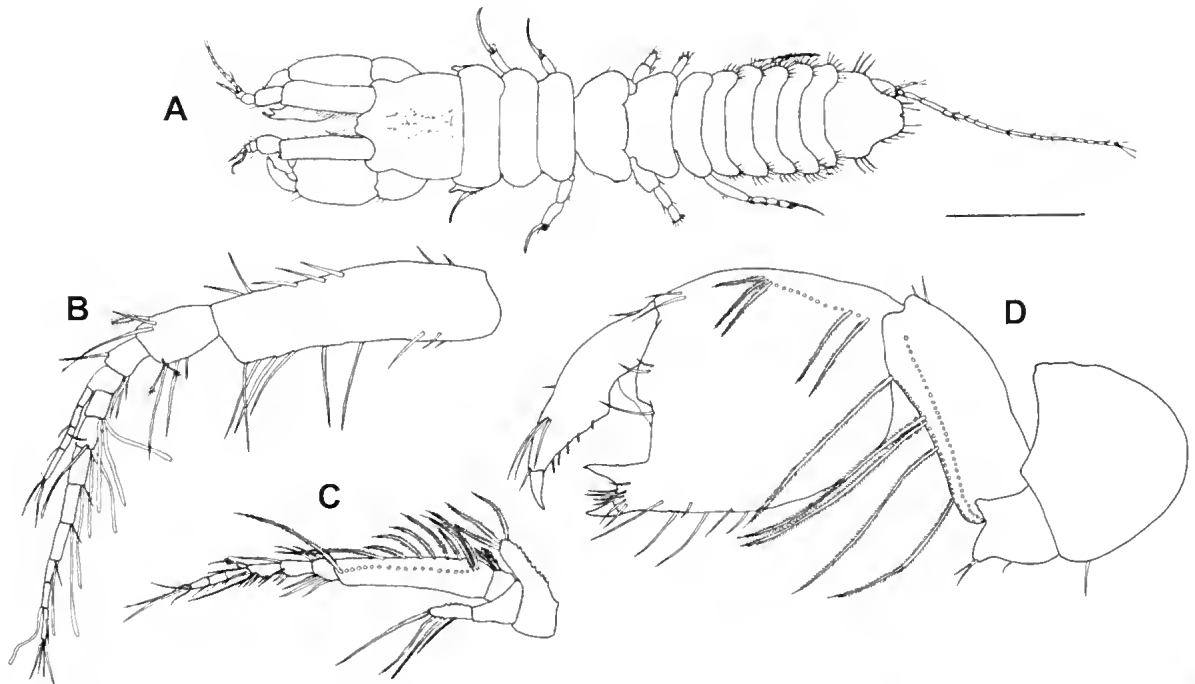
FIG. 2. *Transkalliapseudes banana* sp. nov.: **A**, male holotype, dorsal; **B**, male antennule; **C**, antenna; **D**, male right cheliped. Scale bar =1 mm for A; 0.3 mm for B–D.

longest of these as long as first four segments of flagellum together. Flagellum of six segments, first three with outer expansion bearing three shorter setae, third with single longer outer distal seta as long as three distal segments together.

Mouthparts closely similar to those of *T. spinulata*, but labrum naked; single-articled mandibular palp bearing 28 plumose filtering setae, distal spine 3.2 times as long as its maximum width; labial palp with pronounced, acuminate inner distal apophysis but no mesial or proximal setae; maxillule inner endite with three 1 simple and three setulate spines; second, third and fourth articles of maxilliped palp respectively with 30, 56 and 38 plumose filtering setae in two parallel rows; maxilliped endite with short, simple distal spines, inner caudal spine similar.

Cheliped (Fig. 2D) with stout basis 1.2 times as long as wide, without exopodite or midventral seta, with single simple ventrodistal seta; merus quadrangular with one shorter mid-ventral and two longer ventrodistal setae; carpus elongate, 2.6 times as long as wide, with two parallel rows of 34 (inner) and 29 (marginal) plumose

filtering setae, increasing in length distally along carpus until equal to carpus length. Propodus stout, robust, as long as wide, with 16 inner plumose filtering setae on dorsal margin, decreasing in length distally along propodus and all shorter than half propodal width; fixed finger with large tooth-like apophysis on cutting edge and smaller sharp apophysis adjacent to dactylus; dactylus (moveable finger) with ventral stout setae but no serrations.

Pereopod 1 (Fig. 3A) with stout basis 2.1 times as long as wide, dorsal margin smooth, with dorsoproximal apophysis visible dorsally on whole animal (Fig. 2A), without exopodite; short ventrodistal spine and fine adjacent seta. Ischium with single seta. Merus shorter than basis with short ventral setae in proximal half, with single ventrodistal and dorsodistal spines, the former with marginal denticulation. Carpus compact, with single dorsodistal blunt simple spine, two ventrodistal marginally-denticulate spines, outer face with diagonal row of crenulation. Propodus with four ventral denticulate blunt spines, two dorsodistal denticulate spines; outer face with diagonal row of crenulation,
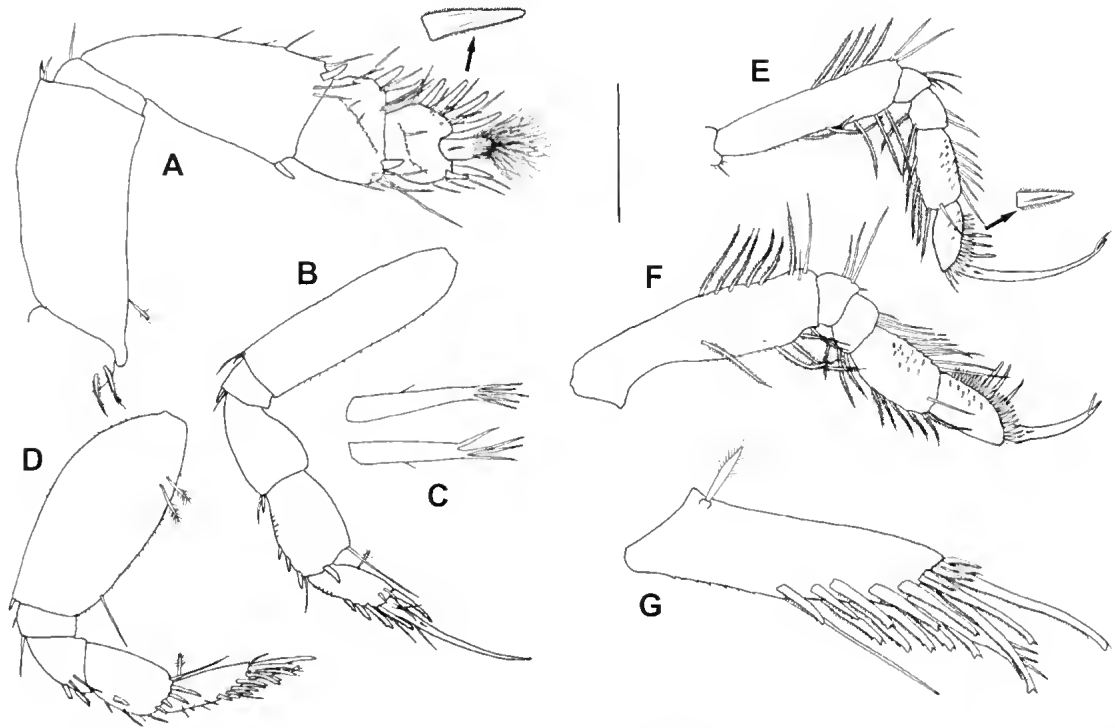
FIG. 3. *Transkalliapseudes banana* sp. nov.: **A**, pereopod 1, with detail of denticulate spine; **B**, pereopod 2; **C**, dactyli of pereopods 4 and 5; **D**, pereopod 4; **E**, male pereopod 6, with detail of denticulate leaf-like spine; **F**, female pereopod 6; **G**, distal articles of pereopod 5. Scale bar = 0.3 mm for A, B, D–F; 0.1 mm for C, G.

inner face with row of six denticulate setae at base of dactylus. Dactylus stout, with proximal seta and distal brush of numerous sensory setae typical of the subfamily.

Pereopod 2 (Fig. 3B) basis 3.6 times as long as wide with sparse fine spinules on dorsal margin, ischium and merus with slender spine and fine seta ventrodistally; carpus as long as merus with sparse comb-rows of spinules proximo-ventrally, three ventral denticulate spines in distal half, one inner distal denticulate spines, dorso-distal seta 1.3 times as long as propodus; propodus 0.8 times as long as merus, with sparse comb-rows of spinules proximoventrally, row of four ventrodistal and one dorsodistal finely denticulate spines; dactylus and unguis fused, slender, twice as long as propodus, with proximal sensory lobe bearing two setae and single simple seta distal to this lobe. Pereopod 3 similar to pereopod 2 but with three inner distal spines on carpus

Pereopods 4 and 5 (Fig. 3D, G) similar to each other; basis 2.15 times as long as wide, with

sparse fine spinules on dorsal proximoventral margins, ventrodistal spine, two dorsoproximal plumose sensory setae and subdistal dorsal seta; merus with two ventrodistal denticulate spines; carpus twice as long as merus, with graded row of four denticulate distal spines as well as mid-ventral small spine; propodus with dorso-proximal plumose sensory seta, four dorsodistal short denticulate spines and distal crown of 15 longer denticulate spines (shorter proximally) each with distal seta; dactylus terminating in four (pereopod 4) or five (pereopod 5) filaments but not a 'brush' of setae (Fig. 3C).

Pereopod 6 (Fig. 3E) smaller and more slender than preceding; basis 4.5 times as long as wide, with sparse fine spinules on dorsal margin, dorsally with five plumose setae in distal half, ventrally with four plumose setae in distal half and two ventrodistal simple setae; ischium shorter than merus with simple ventrodistal setae; merus with two dorsal plumose setae, two ventral simple setae; carpus with four dorsal plumose setae, six ventral simple setae and
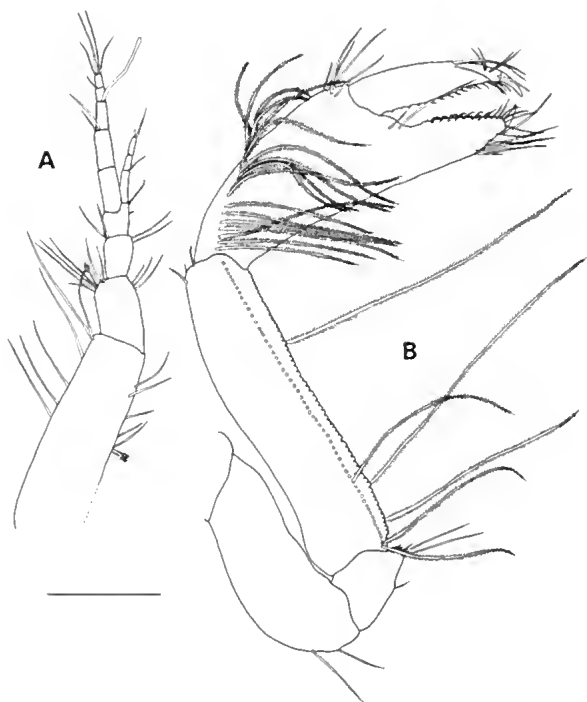
FIG. 4. *Transkalliapseudes banana* sp. nov., female allotype: **A**, antennule (drawn *in situ*); **B**, left cheliped (most carpal filtering setae shown only by their bases). Scale bar = 0.3 mm.

sparse comb-rows of spinules mesially; propodus with sparse comb-rows of spinules mesially, dorsodistal denticulate spine, ventral marginal row of 16 denticulate leaf-like spines and four longer adjacent simple blunt spines; dactylus and unguis fused, twice as long as carpus, distally bifurcate.

Pleopods all alike, typical for the subfamily, basis with three inner plumose setae, exopod smaller than endopod, respectively with 14 and 15 plumose setae.

Uropod biramous, basis with two simple distal setae, exopod shorter than basis and of three segments, endopod elongate, filiform, multi-segmented, 2.8 times as long as pleon (Fig. 2A).

Description of Female. (Only one female specimen, the allotype, had an undamaged anterior). Similar to, but larger than, the male, with sexual dimorphism shown in the antennule, antenna, cheliped and pereopod 6. Length of allotype 5.9 mm. Rostrum truncate rather than concave. Antennule (Fig. 4A) with fewer pinnate sensory

setae than male, accessory flagellum of 3 segments, main flagellum of 5 segments with single aesthetasc on segment 3. Antenna with longer setae than that of male, squama with 6 marginal setae. Cheliped (Fig. 4B) basis more elongate, twice as long as wide; carpus elongate, 4.25 times as long as wide, with two parallel ventral rows each of 59 long, plumose setae; palm of chela (propodus) nearly twice as long as wide, longer than fingers, with dorsodistal tuft of 5 simple setae and, in proximal half, dorsal marginal row of 18 plumose filtering setae, most longer than width of propodus; fixed finger with nine ventrodistal setae in two rows, cutting edge with short spines interspersed with fine denticles and parallel row of short setae; dactylus with dorsal group of four simple setae in distal half and subdistal group of 5 finer setae adjacent to unguis. Sixth leg (Fig. 3F) similar to that of male, with few additional setae as figured commensurate with its larger size; dactylus and unguis as long as carpus.

Etymology. Named after Banana Bank, a submerged bank in Moreton Bay near which all the specimens were collected. Used as a noun in apposition.

Remarks. *Transkalliapsendes* was recently erected by Drumm & Heard (2006b) for their species *T. spinulata* from the shelf off northwestern Western Australia, at 44–82 m depth. It is distinguished from the other genera in the Kalliapseudinae by a combination of characters including the absence of exopodites on both the cheliped and the first pereopod, the presence of vestigial sensory organs (digitiform lobe) on the dactyli of pereopods 2 and 3, the dactyli of pereopods 4 and 5 not reduced to a blunt setose brush and the presence of plumose filtering setae on the distal peduncle article of the antenna.

Transkalliapseudes banana sp. nov. is generally similar to the generotype *T. spinulata* (known only from males), but can be distinguished on a number of characters, notably the distinctly bilobed, or concave, rostrum in the male (not found in any other member of the subfamily), also in the lack of dorsal setae on the pleonites (two pairs on each in *T. spinulata*), in having four segments in the accessory flagellum of the male antennule (three in *T. spinulata*), only three plumose setae on the inner process on proximal

peduncle article of the antenna (four), a naked labrum and mesial face of labial palp, the short plumose filtering setae on the male cheliped propodus (as long as propodal width in *T. spinulata*), far sparser spinulation on the bases of the pereopods, a conspicuous proximal apophysis on the basis of pereopod 1, the presence of only two setae on the sensory lobe of the dactyli of pereopods 2 and 3 (three), the shorter dactylus plus unguis on pereopod 2 (twice as long as propodus, compared with 2.75 times as long in *T. spinulata*), and in having three plumose setae on the pleopod basis (2 in *T. spinulata*).

The only species of *Kalliapseudes sensu* Guţu (2006) described previously from Australia are *K. struthi* Bamber, 2005, from Esperance, Western Australia, *K. multiarticulus* Guţu, 2006, from Darwin, Northern Territory, *K. langi* Guţu, 2006, from Middle Banks, Moreton Bay, and *K. obtusifrous* (Haswell 1882), from Port Jackson, New South Wales (valuably redescribed by Drumm & Heard, 2006a, who gave an identification key to the Australian species of *Kalliapseudes*). The antenna of *K. multiarticulus* was not described, but the species is quite distinct from *T. banana* sp. nov. in having stout, brush-like, sensory dactyli on pereopods 4 and 5, and in having 12 segments in the main flagellum and seven in the accessory flagellum of the antennule. *K. obtusifrons* also has stout, brush-like, sensory (penicillate *sensu* Haswell 1882) dactyli on pereopods 4 and 5 and three segments in the uropod exopod.

Both *Kalliapsendes struthi* and *K. langi* are as small as *T. banana* (all other species being larger at maturity), but they have exopodites on both cheliped and pereopod 1, and a simply convex rostrum (distinctly bilobed [male] or truncate [female], in *T. banana*). Unlike the other two, *K. struthi* does not show fusion of the third and fourth peduncle articles of the antenna (having two short articles after that bearing the squama). The merus of pereopods 2 and 3 is shorter than the carpus in *K. langi* (subequal in length in *K. banana*), and the plumose dorsal setae on the articles of pereopod 6 of *T. banana* are absent in *K. langi*.

The lack of exopodites on both cheliped and pereopod 1 is characteristic of the genus *Mesokalliapseudes*, but those species have a distinct cheliped morphology with an elongate, slender propodus and unequal fingers of the chela, as well as dactyli of pereopods 4 and 5 reduced to a bunt, setose brush. *Cristapseudes* Băcescu, 1980 is also without exopodites, but the other characters which distinguish *Cristapseudes* (complex epignath, no vestigial sensory organs on the dactyli of pereopods 2 or 3, enlarged coxa and reduced dorsodistal spines on the carpus and propodus of pereopod 1) are not found in *Transkalliapseudes*. A key to the current genera of the Kalliapseudinae is given by Drumm & Heard (2006b).

Family Metapseudidae Lang, 1970

Subfamily Synapseudinae Guţu, 1972

Curtipleon Băcescu, 1976(b)

***Curtipleon loerzae* sp. nov.**

(Figs 5–7)

Material Examined. HOLOTYPE: QM-W28079, brooding ♀, PARATYPES: NHM 2006.1530–1533, ♂, 3♀♀ (1 brooding), among the algae *Amphiroa fragilissima*, with *Asparagopsis taxiformis* and *Zonaria diesingiana*, Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8–15 m, 17.02.2005. QM-W28080, ♂ (allotype), 2 ♂♂, subadult ♂, 2♀♀, 3 juvs. QM-W28081, ♀ with oostegites, dissected, in *Phoronis* tube mat, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28082, 3 ♀♀, sponge and bryozoan epifauna, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28083, ♀, amongst sponge, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. All diver collected, A-NL.

Description of Female. Body (Fig. 5A) strongly calcified, typical of the genus, tapering from anterior to posterior; small, holotype 2.28 mm long. Cephalothorax rectangular, naked, sculptured, as long as wide, with concave anterior margin without rostrum; small tubercle either side of anteromedian groove, mid– to posteromedian ridge; eyelobes present, eyes with dark pigment. Six free pereonites; pereonites 1 and 2 shorter than wide with convex lateral margins, swollen laterally and with median ridge; pereonite 3 as pereonite 2 but longer and without ridge, with small anterolateral spine-like apophyses; pereonite 4 longest (1.5 times as long as pereonite 1) with small anterolateral spine-like apophyses, narrower anteriorly, median round tubercle and posterior square tubercle;
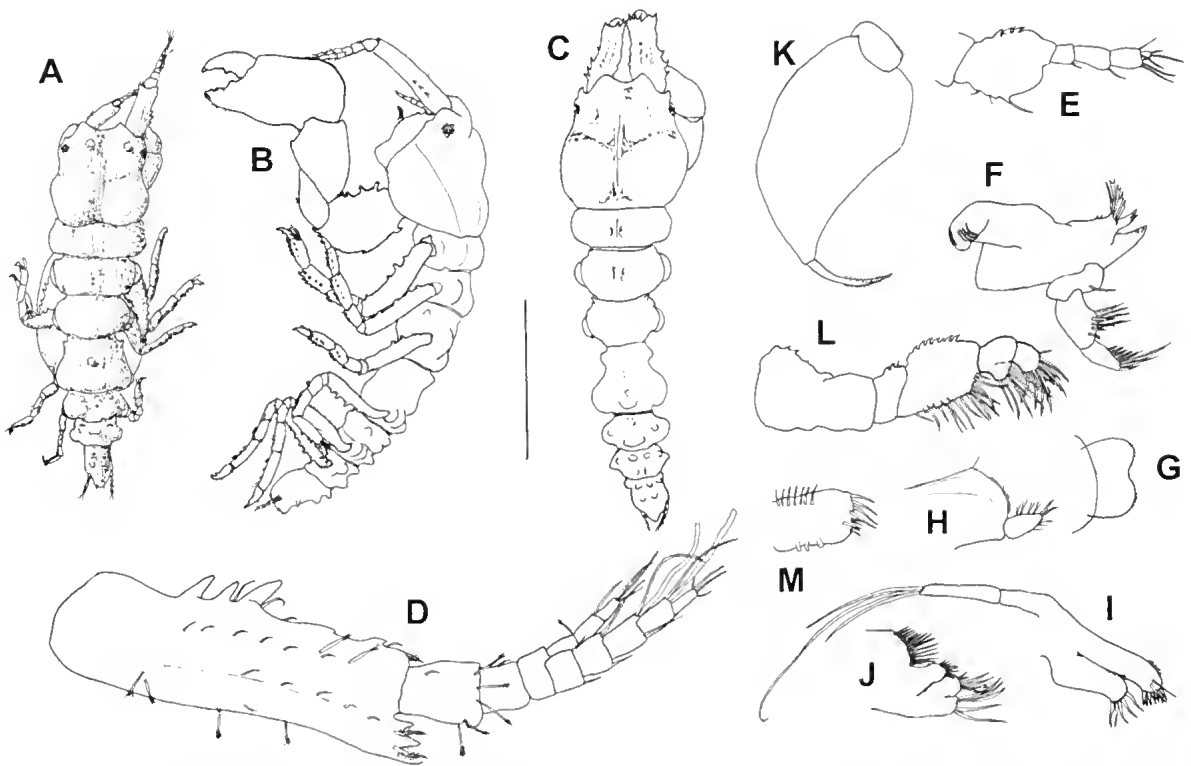
FIG. 5. *Curtipleon loerzae* sp. nov.: **A**, holotype female, dorsal; **B**, allotype male, lateral; **C**, allotype male, dorsal; **D**, antennule; **E**, antenna; **F**, right mandible; **G**, labrum; **H**, labium; **I**, maxillule; **J**, maxilla; **K**, epignath; **L**, maxilliped palp; **M**, maxilliped endite. **D–M**, paratype female with oostegites. Scale bar = 1 mm for A, B, C; 0.2 mm for D–M.

pereonite 5 0.75 times as long as pereonite 1, with four small, round anterior tubercles and midposterior squared tubercle; pereonite 6 shorter than pereonite 5 with midlateral rounded tubercles and posterior squared tubercle. Pleon of five pleonites and pleotelson all fused, 0.6 times as wide as long with four dorsal rounded tubercles. Live colour mainly grey, cephalon pink, antennae olive-green.

Antennule (Fig. 5D) proximal peduncle article robust, 3.2 times as long as wide, with three outer spine-like apophyses in proximal half; inner distal corner extended into trifid spine-like apophysis; simple, shorter, curled setae and sensory plumose setae numerous, as figured. second article 0.2 times as long as first with distal crown of five plumose sensory setae; third article half as long as second, fourth article one-third length of second. Main flagellum of five segments subequal in length, distal segments narrower than proximal, fourth and fifth

segments with single aesthetasc, distal segment with four short distal setae; accessory flagellum of three segments.

Antenna (Fig. 5E) with five-articled peduncle; proximal article short, naked; second article expanded, as wide as long, with inner spine-like apophyses and outer setae on small tubercles; squama absent. Third article one-quarter as long as second with single outer seta, fourth article twice as long as third with single outer seta; fifth article just shorter than fourth with three outer and single inner distal setae. Flagellum of one tiny segment with two distal setae.

Labrum (Fig. 5G) bilobed, rounded, laterally setulose. Mandible (Fig. 5F) with tricuspid pars incisiva, bicuspid lacinia mobilis, setiferous lobe with five setae, pars molaris slender, blunt but with finely denticulate margin; palp of three articles, proximal article with simple seta, second article articulating anaxially on first, as long as first with two rows each of four denticulate

FIG. 6. *Curtipleon loerzae* sp. nov.: **A**, left cheliped of allotype male; **B**, distal articles of right cheliped of allotype male; **C**, right cheliped of paratype female; **D**, right uropod. Scale bar = 0.3 mm.

gate, simple. Epignath (Fig. 5K) large, cup-shaped, with setulose distal seta.

Cheliped (Fig. 6C) basis 1.6 times as long as wide, dorsal margin with four spine-like apophyses interspersed with setae; ventral margin with small proximal apophysis, single median and three distal spine-like apophyses each with adjacent fine seta; exopodite absent. Merus quadrangular, with single ventromedian spine-like apophysis, few setae; carpus slender, 2.2 times as long as wide, with sparse, fine setae as figured; propodus rounded, 1.5 times as long as wide, fixed finger half length of body of propodus, with finely crenulate cutting edge, three ventral setae; dactylus robust with fine cigar-shaped setae along cutting edge. Finger tips opposed.

Pereopods all broadly similar to each other. Pereopod 1 (Fig. 7A) coxa with slight setose apophysis; basis slender, 4 times as long as wide, without exopodite; dorsal margin with three mesial and one subdistal rounded linguiform apophyses interspersed with fine, simple setae; ischium stout, naked; merus 0.3 times as long as basis, with paired subdistal, ventral spines with finely denticulate proximal margin; carpus and propodus subequal, 1.3 times as long as merus, each bearing two ventral rows of triangular finely-denticulate spines and sparse simple setae as figured; propodus with ventrodistal plumose seta, dorsodistally with spine and cluster of five setae, three being simple, two with comb-like denticulation. Dactylus stout, ventrally with proximal curved and distal pointed apophyses and three fine inner setae, dorsally with paired fine setae; unguis distinct, stout.

Pereopod 2 (Fig. 7B) as pereopod 1 but smaller, with single simple distal seta on propodus and dorsal plumose sensory seta; merus 0.8 times as long as propodus. Pereopod 3 (Fig. 7C) shortest pereopod, particularly basis, otherwise as pereopod 2. Pereopod 4 (Fig. 7D) as pereopod 2 but merus and propodus subequal, spines on propodus reduced to a single row, propodus with dorsodistal pair of spines and one simple and two comb-like setae; pereopod 5 (Fig. 7E) as pereopod 2 but with single spine row on carpus, denticulate spines more slender; pereopod 6 (Fig. 7F) as pereopod 5 but with fewer ventral denticulate spines.

inner setae, dorsal setae shorter, third article shorter than second, with graduated row of eight denticulate setae in distal half.

Labium (Fig. 5H) with smooth outer margin, palp with two distal setae. Maxilla (Fig. 5J) with rostral row of 15 setae; endites with simple setae. Maxillule (Fig. 5I) inner endite with five simple distal setae and slight inner apophysis, outer endite with two subdistal setae and seven distal spines, inner mesial and outer distal margins sparsely setose; palp of two articles, distally with three simple, long setae. Maxilliped (Fig. 5L) basis naked; palp proximal article with paired outer spine-like apophyses; second article outer margin coarsely denticulate, inner margin with outer row of 14 simple setae and inner row of five or six fine setules; third article with distinct inner apophysis bearing six simple setae; distal article with eleven setae in two rows, proximal setae finely denticulate; endite (Fig. 5M) with simple four longer outer and four shorter inner distal simple setae, subdistal seta slender, elon-

FIG. 7. *Curtipleon loerzae* sp. nov.: **A–F**, pereopods 1–6 respectively. Scale bar = 0.2 mm.

Pleopods absent.

Uropods (Fig. 6D) short, uniramous, basis simple, endopod of three segments, distal segment with four simple and one plumose sensory setae.

Holotype with eight embryos in brood pouch.

Description of Male. Broadly similar to, but larger than, female, allotype (Fig. 5B, C) 2.8 mm long. Lateral carina on carapace conspicuous. Antennule similar, but main flagellum segments 1–4 with 1, 1, 2 and 1 aesthetascs respectively. Major dimorphism shown by chelipeds, both of which are more robust in the male. Left cheliped of allotype (Fig. 6A) larger than right. Basis dorsally with two parallel rows of spine-like apophyses and rounded group of linguiform apophyses distally; ventral proximal apophysis spine-like. Carpus stout, 1.2 times as long as wide; propodus massive, as long as merus and carpus together, stout dactylus with tooth-like apophyses on cutting edge. Right cheliped of allotype (Fig. 6B) smaller than left, more similar to that of female, although larger and more robust; dactylus without tooth-like apophyses.

Etymology. Named for Dr Anne-Nina Lörz, who collected all the *Curtipleon* material as well as so many other specimens reported herein.

Remarks. Three species of the distinctive genus *Curtipleon* had been described, and they were reviewed by Larsen (2002). *C. carinata* (Makaveeva, 1971) was recorded from the Gulf of Aden at 50 m depth, *C. carinatoides* (Băcescu, 1976) from Tanzania at 25–40 m depth, and *C. heterochelatum* Larsen, 2002, from the Andaman Sea at 18–26 m depth. The last is best-described, the first the worst. Including the present species, the distribution of the genus is in keeping with the zoogeographic trends described by Bamber (1998).

All the previous species have denticulation along the anterior margin of the cephalic depression, *C. carinatoides* having large lateral and central spine-like apophyses, the other two having smaller crenulation. There are no spine-like apophyses indicated by Makaveeva for *C. carinatus*; conversely, the spination of the antennular peduncle is far greater than that of *C. loerzae* sp. nov. *C. heterochelatum* is distinct in having a large spine-like apophysis dorsodistally on the cheliped carpus of the male. *C. loerzae* has a smooth anterior to the cephalon, cheliped basis apophyses reminiscent of those of *C. carinatoides*, and no dorsodistal apophysis on the cheli-

ped carpus; the antennal structure appears also to be unique, although all the previous descriptions and figures of antennae are unclear.

All species show the sexual dimorphism in the chelipeds, those of the male being larger and more robust. Both Băcescu (1976a: 'hundreds' of specimens) and Larsen (2002: one male) note that the left cheliped of the male is larger and more massive than its right cheliped. The male specimen of *C. loerzae* from Flat Rock and one of the non-allotype males from the Point Lookout *Phoronis* tube-mat have their right chela larger than the left; in all other males, including the allotype, the left cheliped is larger than the right.

All the present specimens were found in epifaunal communities, at between 8 and 15 m depth off the north of North Stradbroke Island (and always sympatric with *Konarus cheiris*, q.v.).

Family Parapseudidae Guțu, 1981

Longiflagrum Guțu, 1995

Longiflagrum caeruleus (Boesch, 1973)

Apseudes caeruleus Boesch, 1973: 168–174, figs 1–3.

Material Examined. QM-W28084, 2 ♂♂, 14 ♀, 11 juvs, NHM 2006.1534–1539, 2 ♂♂, 2 ♀, 2 juvs, sandy mud (40:55) with *Caulerpa taxifolia*, Moreton Bay, 27°31.58'S, 153°24.18'E, 3.9 m, 35‰, 28.8°C, 11.02.2005, van Veen grab, RNB. QM-W28085, topotypic juv., littoral sand with *Halophila ovalis*, Bradbury Beach, Dunwich, North Stradbroke I., Moreton Bay, 27°29.6'S, 153°23.8'E, +0.4 m, 13.02.2005, trowel sample, RNB. QM-W28086, ♀, Zosteretum inside sand bar, Amity Point, North Stradbroke I., Moreton Bay, 27°24.7'S, 153°26.15'E, depth 0 m, 35.5‰,14.02.2005, spade sample, RNB. QM-W7409, ♂, 3 ♀♀, Woogoompah I., southern Moreton Bay, amongst *Zostera* 'below low water', 11.04.1976, Australian Littoral Society.

Remarks. The type locality for *Longiflagrum caeruleus* is Dunwich, Moreton Bay, from intertidal sediments with eelgrass. It is thus reassuring to find the species still present in large numbers. Live adult specimens are a pronounced cerulean blue (hence the name) while the manca is white.

Longiflagrum estuarius (Boesch, 1973)

Apseudes estuarius Boesch, 1973: 174–181, figs 4–6.

Material Examined. QM-W7124, over 100 specimens, including ♂ and ♀, 3.2 km from the mouth of the Serpentine Creek, Brisbane, 20.08.1974, T.P. Tebble & PJFD.

Remarks. *L. estuarius* was originally described from the estuaries of the Brisbane (type locality) and Fitzroy Rivers. Although not collected during the 2005 surveys, which concentrated on fully marine habitats, it continues to be common in the mainland estuaries feeding into Moreton Bay (P. Davie pers. comm.). As well as their habitat differences, the morphological differences listed by Boesch (1973) (*L. estuarius* having a much shorter uropod, fewer ventral spines on the propodus of pereopod 1, and no ventral hyposphenia on the pereonites) allow easy distinction of the two Australian species of *Longiflagrum*.

Remexudes toompani Błażewicz-Paszkowycz & Bamber, 2007

Remexudes toompani Błażewicz-Paszkowycz & Bamber, 2007a: 19–25, figs 10-12.

Material Examined. All of this material formed part of the type series and is described in Błażewicz-Paszkowycz & Bamber (2007a); it is listed here for completeness of the Moreton Bay material. PARATYPES: QM-W28150, 3 ♀♀ without oostegites, 2 ♀♀ with oostegites, 2 ♂♂, clean medium sand with some shell and ophiuroids, off South Passage East of Moreton I., 27°17.65'S, 153°26.95'E, 19.4 m. QM-W28151, 2 ♂♂, 5 ♀♀, clean medium sand WNW of Flat Rock, off South Passage East of Moreton I., 27°24.10'S, 153°29.18'E, 10.7 m. NHM 2006.15078-1514, 4 ♂♂, 4 ♀♀ without oostegites, clean medium sand WNW of Flat Rock, off South Passage East of Moreton I., 27°23.46'S, 153°30.08'E, 20 m. QM-W28152, ♂, brooding ♀, ♀ with oostegites, ♀ without oostegites, slightly muddy medium sand with holothurians, WNW of Flat Rock, off South Passage East of Moreton I., 27°22.95'S, 153°30.79'E, 26.6 m. All 19.02.2005, van Veen grab, RNB. QM-W28153, 2 ♂♂, 5 ♀♀ (4 of these with oostegites), clean medium sand East of Moreton I., 27°18.19'S, 153°27.56'E, 20.6 m; ♀ without oostegites, clean medium sand East of Moreton I., 27°18.37'S, 153°26.77'E, 9.9 m; both 22.02.2005, van Veen grab, RNB.

Remarks. This taxon shows affinities with *Pakistanapseudes* (see below) and, *Saltipedis* Guțu, 1995, but is distinguished principally in having a swimming morphology to the second pereopod, with merus, carpus and propodus wide and flattened in the same manner as pereopod 1 of most parapseudids; additionally, the propodus of pereopod 1 is twice as long as wide. All the present material was collected from east of the

South Passage, either north of North Stradbroke Island or east of the southern tip of Moreton Island, on clean medium sand substrata from depths of 10–27 m. The other material in the type series, held in the Museum Victoria, Melbourne, was collected from the Bass Strait.

Pakistanapseudes Băcescu, 1978

Pakistanapseudes australianus Guţu, 2006

Pakistanapseudes australianus Guţu, 2006: 260–264, figs 511–525; Błażewicz-Paszkowycz & Bamber, 2007a: 12–14, fig. 6.

Material Examined. QM-W28154, ♀ with oostegites, sandy mud, Moreton Bay, 27°22.72'S, 153°19.43'E, 15 m, 35‰, 29.4°C. QM-W28155, ♀?, no legs muddy sand with spatangoids, Moreton Bay, 27°20.91'S, 153°19.96'E, 16.6 m, 33‰, 29.1°C. 1 damaged specimen, amongst *Halophila decipiens* on sand with some shell, west side of Moreton I., Moreton Bay, 27°16.90'S, 153123.20'E, 4.7 m, 35‰, 28.6°C. All 10.02.2005, van Veen grab, RNB. QM-W28465, 3 ♀♀, 1 brooding, MBWS Stn. 2. QM-W28466, ♀, MBWS Stn. 5. QM-W28467, 3 ♀♀?, 1 brooding, MBWS Stn. 6. QM-W28468, ♀, MBWS Stn. 7. QM-W28469, ♂, MBWS Stn. 8. QM-W28470, ♀ with empty brood pouch, MBWS Stn. 12. QM-W28471, brooding ♀, MBWS Stn. 13. All van Veen grab, PJFD. QM-W28167, ♀, Middle Banks, northern Moreton Bay, 17.09.1983/13.01.1984, P. Saenger & S. Cook (there are two dates on the label, in material containing a number of species).

Remarks. *P. australianus* is one of five described species of the *Pakistanapseudes*-group (*sensu* Błażewicz-Paszkowycz & Bamber, 2007a) with a pointed rostrum and pigmented eyes and a simple dactylus and unguis to pereopod 2. However the other four species — *P. hodgsoni* Bamber, 2000, from Hong Kong, *P. shiinoi* Băcescu, 1978, from the Gulf of Aden, *Biropalostoma spiniferum* Guţu & Angsupanich, 2004, and *P. pectinis* (Bamber, 1998)(see below) from Brunei — all have a rostrum with rounded 'shoulders' either side of a terminal point, unlike the present species. Other differences between these taxa are discussed in Błażewicz-Paszkowycz & Bamber (2007a). *P. australianus* was taken from muddier substrata than the following species. Moreton Bay is the type locality for this species (Guţu 2006).

Guţu (2006) moved *P. pectinis* from *Pakistanapseudes* to his new genus *Platylicoa*, together with his new species *Platylicoa setosa*. The problems with the genus *Platylicoa* are discussed by Błażewicz-Paszkowycz & Bamber (2007a).

Pakistanapseudes perulpa Błażewicz-Paszkowycz & Bamber, 2007

Pakistanapseudes perulpa Błażewicz-Paszkowycz & Bamber, 2007a: 3–8, figs 1-3.

Material Examined. all of this material formed the type series and is described in Błażewicz-Paszkowycz & Bamber (2007a). HOLOTYPE: QM-W28156, ♀ with oostegites and antennule, clean medium sand with shell breccia, N. of Moreton I., Moreton Bay, 26°56.62'S, 153°24.35'E, 27.9 m, 16.02.2005. QM-W28157, allotype ♂, clean medium sand with some shell and ophiuroids, off South Passage East of Moreton I., 27°17.65'S, 153°26.95'E, 19.4 m. NHM 2006.1515, ♂, clean medium sand East of Moreton I., 27°13.70'S, 153°26.84'E, 25.2 m. QM-W28158, brooding ♀, clean medium sand with holothurians, east of Moreton I., 27°18.19'S, 153°27.56'E, 20.6 m. QM-W28159, 2 ♀♀, (1 brooding) fine sand with shell and *Nephtys* sp., west of the northern end of Moreton I., 27°12.37'S, 153°21.42'E, 16.8 m, 23.02.2005. QM-W28160, 3 ♀♀ (2 brooding, 1 dissected) clean sand with polychaetes, west of Moreton I., 27°04.41'S, 153°17.36'E, 7.2 m, 23.02.2005. NHM 2006.1516-1519, 4 ♀♀ (1 brooding) medium sand with shell, west of Moreton I., 27°04.10'S, 153°16.95'E, 8.5 m, 23.02.2005. QM-W28161, ♀ with empty brood pouch medium sand with coarse shell breccia, callianassids and ophiuroids, southeast of Bribie I., 27°03.17'S, 153°13.17'E, 10.2 m, 23.02.2005. All van Veen grab, RNB.

Remarks. The only other *Pakistanapseudes*-group species with a rounded rostrum, pigmented eyes and simple (not bifurcate) claw on pereopods 2 and 3 are the generotype, *P. leptochelatus* Băcescu, 1978 from the Gulf of Oman, *P. bassi* Błażewicz-Paszkowycz & Bamber (2007a) from Bass Strait, Australia, and *Thaicungella lideeiensis* Guţu & Angsupanich, 2004 from Thailand. *T. lideeiensis* is the only species in the group to have multiple setae on the dactylus of all pereopods other than the fourth; unlike *P. perulpa*, it has a compound dactylus and claw on pereopod 4. *P. perulpa* is distinct from *P. leptochelatus* in having far more setae on the antennal squama, far more aesthetascs on the male antenna, five distal setae on the maxillule palp, marginal spines on the articles of the pereopods, more distal setae the exopodites of the cheliped and pereopod, and more segments in the uropod exopod. *P. perulpa* is distinguished from the only other Australian species of a similar morphology, *P. bassi* by having setae on both margins of the pleopod bases (dorsal only in *P. bassi*), pereonites 5 and 6 wider than long (longer than wide in *P. bassi*), and distally blunt marginal

spines on pereopod 1 propodus (distally pointed in *P. bassi*).

The present material was collected from outside Moreton Bay itself around Moreton Island (east, north and west), from clean sand substrata, usually containing shell breccia, and at depths from 7–28 m.

Pakistanapseudes turkoroa
Błażewicz-Paszkowycz & Bamber, 2007

Błażewicz-Paszkowycz & Bamber, 2007a: 8–12, figs 4,5.

Material Examined. This material is described in Błażewicz-Paszkowycz & Bamber (2007a). HOLOTYPE: QM-W28162, ♂, muddy sand with fine shell breccia, Moreton Bay, 27°28.66'S, 153°21.34'E, 7.2 m, 35‰, 29°C, 11.02.2005, van Veen grab, RNB.

Remarks. This species, known only from the holotype male, is distinct in the genus in having a truncate, flattened rostrum. The first pereopod bears unique fleshy dendritic structures on the ventral margins of the merus, carpus and propodus and distally on the dactylus; they are assumed to have some sensory function, and may be absent in the female. It is further distinguished from the other Australian species of this genus by having a much more robust cheliped, that of those other species being extremely slender. The specimen is from shallow muddy sand just north of Peel Island ('Turkrooa', from which its specific epithet derives). An identification key to the Australian species of *Pakistanapseudes* is given by Błażewicz-Paszkowycz & Bamber (2007a).

Family Pagurapseudidae Lang, 1970
Subfamily Pagurapseudinae Lang, 1970

Pagurotanais Bouvier, 1918

Remarks. Guțu (1996) erected *Pagurolangis* for those pagurapseudid species from the Gulf of Mexico and off the Pacific coast of Mexico, which are distinguished by having an exopodite on the cheliped but not on pereopod 1, these being respectively absent and present in species of the other two genera of the Pagurapseudinae, *Macrolabrum* Băcescu, 1976 and *Pagurapseudes* Whitelegge, 1901, although McSweeney (1982) interprets a structure on the cheliped of *Pagurapseudes spinipes* as a rudimentary exopodite. The type species of *Pagurolangis* was designa-

ted as *Pagurotanais bouryi* Bouvier, 1918 — a species for which Bouvier (1918) erected *Pagurotanais* as a new genus. Despite the possibility of 'serious confusion' which Guțu (*loc. cit.*) thought could arise from the suffix 'tanais' alluding to tanaidomorph rather than apseudomorph tanaidaceans, Bouvier's generic name has nomenclatural priority, and *Pagurolangis* Guțu, 1996, is a junior synonym of *Pagurotanais* Bouvier, 1918.

If the rudimentary process on the cheliped of *Pagurapseudes spinipes* is a rudimentary exopodite, this would introduce problems for the generic distinction, as *P. spinipes* is the generotype of *Pagurapseudes*. A further distinction suggested by Guțu (1996) is the width of the basis of pereopod 1, being wider than merus, carpus or propodus in *Pagurapseudes*, but of a similar width in *Pagurotanais*. Unfortunately, again the figures of Whitelegge (1901) indicate a basis little if any wider than the merus for *Pagurapseudes spinipes*.

Pagurotanais koonungai sp. nov.
(Figs 8, 9)

Material Examined. HOLOTYPE: QM-W28087, ♂, amongst algae, Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8–15 m, 17.02.2005, A-NL.

Description of Male. Body (Fig. 8A) typical of a pagurapseudid, pleon skewed to the right and curved under pereon; small, holotype about 2.1 mm long. Cephalothorax subrectangular, as long as wide, with smooth, slightly convex anterior margin; on each side one single, simple subocular seta and paired, plumose midlateral and posterolateral setae. Eyelobes distinguished, eyes present, darkly pigmented. Epistome inconspicuous. Six free pereonites, all with anterolateral and posterolateral plumose setae and paired median anterodorsal simple setae; pereonite 1 shortest, 0.75 times as long as pereonite 2 and 2.8 times as wide as long; pereonites 2–6 subequal, pereonites 4 and 5 just longest. Pleon of five free subequal pleonites, without pleopods, each pleonite about 4.4 times as wide as long, with single plumose midlateral seta and sparse row of simple posterodorsal setae (plumose setae on pleonite 6). Pleotelson (Fig. 8B) subrectangular, longer than last two pleonites together, 1.3 times as wide as long, with mid-lateral and

posterolateral plumose setae and paired simple distal setae.

Antennule (Fig. 8C), proximal peduncle article three times as long as wide, with inner and outer plumose setae but no apophyses; second article one-third as long as first with group of distal plumose sensory setae; third article 0.75 times as long as second, fourth peduncle article 0.4 times as long as third. Main flagellum of three segments, the first two wider than long, with 3, 3 and 2 aesthetascs respectively; accessory flagellum of one segments, distally reaching past second segment of main flagellum.

Antenna (Fig. 8D) with wide proximal peduncle article bearing longer plumose and shorter simple setae distally; second article as long as wide, naked; third article twice as long as second, with plumose sensory seta; fourth peduncle article three times as long as second with two shorter and one longer distal setae. Flagellum of two compact segments, penultimate segment with single seta as long as first three peduncle articles together, distal segment with three distal setae.

Mouthparts generally typical for the subfamily. Labrum rounded, sparsely setose. Left mandible (Fig. 8E) with denticulate pars incisiva, lacinia mobilis conspicuous with four unequal 'teeth', setiferous lobe with four simple or bifid setae; palp of three articles, proximal article with long, plumose distal seta; second article longest, 1.5 times as long as proximal article, with seven small spines in distal half; third article as long as first, with seven progressively longer setae in distal half, distal seta much longer than article. Right mandible as left but without lacinia mobilis. Labial palp with two distal setae. Maxillule (Fig. 8F) inner endite with four simple distal setae, outer endite with 10 distal spines, outer margins sparsely denticulate; palp of two articles with indistinct articulation, distally with three setae (damaged in preparation). Maxilliped (Fig. 8G) endite with slender outer distal setae, blunt inner distal and inner caudodistal spines. Maxilliped basis with paired plumose setae; proximal palp article with simple outer margin with one seta; second article with three long plumose and two shorter simple setae on inner margin, one

shorter and one longer simple setae distally on outer margin; third article with six inner marginal simple setae; distal article with thirteen simple inner-marginal and distal setae. Epignath with robust, setulose distal seta.

Chelipeds (Fig. 9A) showing no conspicuous dimorphism. Compact basis just longer than wide, with mid-ventral and ventrodistal spines and single ventrodistal plumose seta; square apophysis ('sidepiece') at point of attachment but exopodite absent. Merus triangular, ventral margin with two stout plumose setae. Carpus elongate, more than twice as long as wide, widening distally, ventral margin with fine simple setae and single, longer plumose seta. Propodus relatively compact, 1.1 times as long as wide, with two proximal ventral setae and one mid-distal and two dorsodistal setae a base of dactylus; fixed finger with row of small teeth distally on cutting edge and three distal ventral setae; moveable finger curved with two minute spines on cutting edge.

Pereopod 1 (Fig. 9B) longest pereopod, with relatively slender basis 2.5 times as long as wide, dorsal margin bearing nine plumose setae, ventral margin with two curved proximal spines and two distal plumose setae; exopodite absent. Ischium longer than wide with single ventrodistal plumose seta. Merus shorter than basis, ventral margin with four plumose setae, finer simple setae submarginally and proximally and paired spines distally. Carpus as long as merus, with three ventral spines and simple setae, single spine, simple seta and plumose seta dorsodistally. Propodus longer than basis, with four ventral spines and simple setae. Dactylus curved, as long as propodus, with fine ventral setae, unguis slender, 0.5 times as long as dactylus.

Pereopods 2–6 (Fig. 9) similar to each other, progressively shorter, pereopod 2 one-half as long as pereopod 1; bases 1.5 times (pereopod 2) to 1.3 times (pereopod 6) as long as wide, with subdistal, ventral plumose seta on pereopod 2, paired dorsal plumose setae on pereopods 5 and 6; ischium with two (pereopod 2) one (pereopods 3 and 4) or no simple ventrodistal setae. Pereopods 2–4, merus with three rows, carpus with two rows and propodus one row of 'sucker-like' spines; and plumose setae
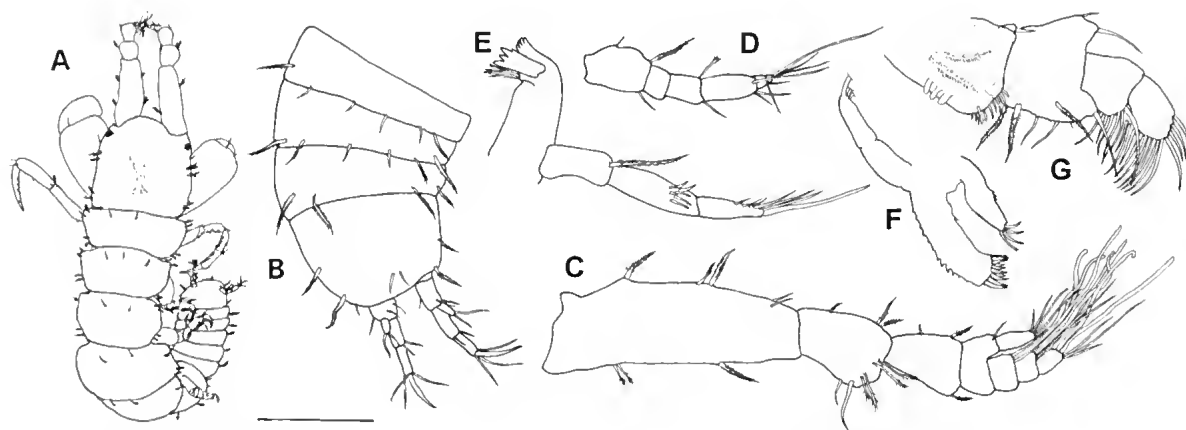
FIG. 8. *Pagurotanais koonungai* sp. nov., male holotype: **A**, habitus; **B**, pleonites 3–5 and pleotelson, dorsal; **C**, antennule; **D**, antenna; **E**, left mandible; **F**, maxillule; **G**, maxilliped. Scale bar = 0.5 mm for A; 0.2 mm for B; 0.15 mm for C; 0.1 mm for D–G.

as figured; merus with dorsodistal plumose seta, ventrodistal plumose setae on pereopods 3 and 4; carpus with dorsodistal plumose seta on pereopod 2, ventrodistal plumose setae on pereopods 3 and 4; propodus with long distal plumose seta on pereopod 2 only. Pereopods 5 and 6, merus short, with two ventrodistal 'sucker-like' spines; carpus and propodus as pereopods 2–4 except carpus with ventrodistal simple spine, propodus of pereopod 6 with denticulate spine adjacent to dactylus (Fig. 9F). Merus about as long as carpus on pereopods 2–4; on pereopods 5 and 6 carpus four times as long as merus. Propodus of pereopod 2 with simple distal seta; propodus of pereopod 6 with distal denticulate spine and adjacent simple spine. Dactylus and unguis fused into claw, with minute inner seta.

Pleopods absent. Uropod (Fig. 8B) biramous, basis with three small distal setae; endopod twice as long as basis, of two subequal segments, second segment distally with three simple setae and one stout distal spine-like seta; exopod of one segment, half as long as proximal endopod segment, with two slender distal setae.

Female unknown.

Etymology. *Koonungai* is a local Australian Aboriginal name for North Stradbroke Island, just off the north coast of which is the type locality of this species.

Remarks. *Pagurotanais koonungai* sp. nov. adds a little confusion to the distinction of the genera *Pagurotanais* and *Pagurapseudes*, in having no exopodite on either the cheliped or pereopod 1. The basis of pereopod 1 is of similar width to the merus, carpus and propodus. The lack of a significant epistome excludes the present species from *Macrolabrum*. With the main and accessory flagella of the antennule having two and one segments respectively, the uropod endopod and exopod having two and one segments respectively, the narrow basis of pereopod 1, and the extreme reduction of the pleopods, the present species is perhaps closest to *Pagurotanais bouryi*. Many of these features are also found in *Pagurapseudes spinipes*, but this generotype and all other species of *Pagurapseudes* have a large, plumose exopodite on pereopod 1, and on that feature alone the distinction of the genus *Pagurotanais* is maintained, and includes the present species.

Pagurotanais koonungai is distinguished from all other species of the genus by the absence of an exopodite on the cheliped, the absence of pleopods, the truncated segments on the main flagellum of the antennule and in the lack of a distinct rostrum.

Suborder TANAIDOMORPHA Sieg, 1980

Superfamily Tanaiodea Dana, 1849
Family Tanaidae Dana, 1849
Subfamily Sinelobinae Sieg, 1980

Sinelobus Sieg, 1980
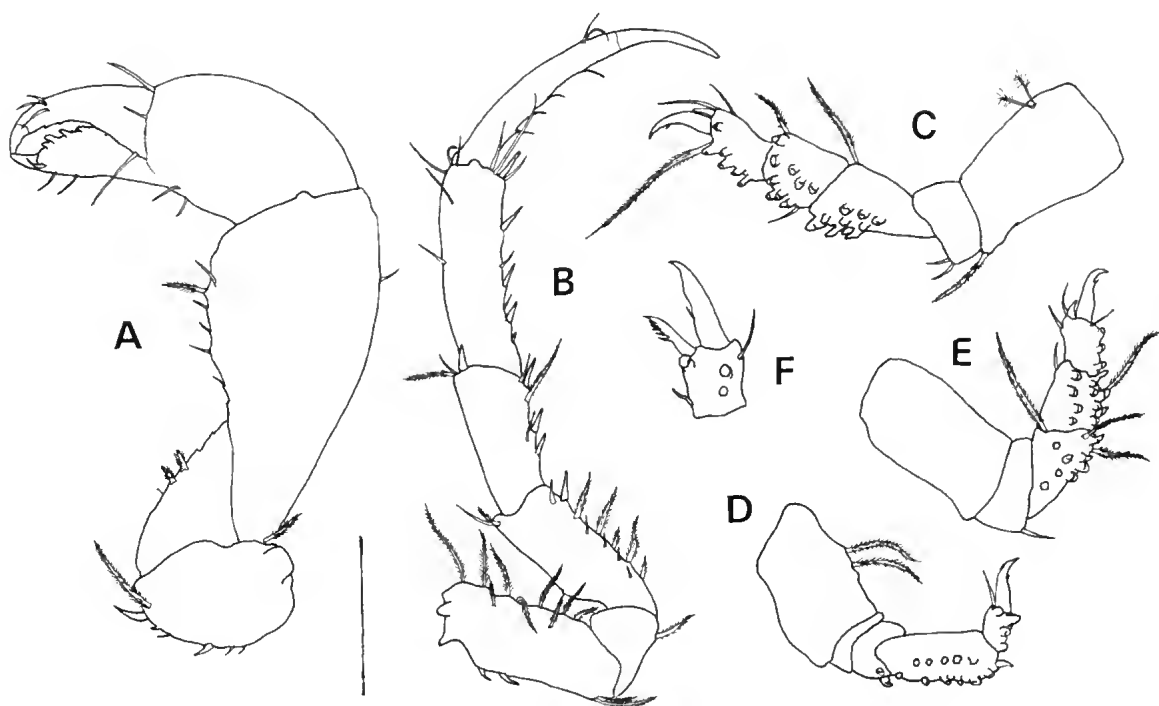
FIG. 9. *Pagurotanais koonungai* sp. nov., male holotype: **A**, right cheliped; **B–E**, pereopods 1, 2, 3 and 5 respectively; **F**, distal articles of pereopod 6. Scale bar = 0.2 mm for A, B; 0.15 mm for C, D, E; 0.1 mm for F.

Sinelobus pinkenba sp. nov.
(Figs 10, 11)

?*Sinelobus stanfordi sensu* Sieg, 1980 (*partim*: Queensland specimens), non *Tanais stanfordi* Richardson, 1901.

Material Examined. HOLOTYPE. QM-W28657, brooding ♀; PARATYPES QM-W15572, 5 ♀♀, 2 ♂♂, all Bulwer I., Brisbane River, in rotting timber near low-tide mark on boat ramp, 12.07.1988. J. Short, J. Johnson & P. Lawless.

Description of female: typical *Sinelobus*, body (Fig. 10A) 3.6 times as long as wide, dorsally with black mottling on cephalon only (in preserved material); length of holotype 4.1 mm. Cephalothorax subrectangular, tapering towards anterior, 1.1 times as wide as long, with slight rounded frons but no rostrum, eyes present, pigmented. Cephalothorax shorter than pereonites 1–3 together. Six free pereonites, rounded laterally, with one small lateral seta on each side, four small dorsal setae on pereonites 1 and 6 towards anterior of pereonite, and paired dorsolateral setae on remaining pereonites; pereonite 1 shortest, half as long as pereonite 3, pereonite 3 1.2 times as long as pereonite 2, pereonites 4 and 5 longest,

1.4 times as long as pereonite 2, pereonite 6 as long as pereonite 3 (all pereonites respectively 3.4, 2.1, 1.7, 1.4, 1.4 and 1.6 times as wide as long). Pleon of four free pleonites with lateral seta on each side and paired dorsolateral setae; pleonites 1 and 2 with transverse latero-dorsal rows of setae not reaching centre of pereonite; pleonites 1 to 3 bearing pleopods; pleonite 4 shorter and narrower, without pleopods. Pleotelson (Fig. 11J) semicircular, 1.6 times as wide as long, with paired lateral and three laterodistal setae on each side and paired distal setae.

Antennule (Fig. 10C) of four articles; proximal article 1.8 times as long as wide with outer distal tuft of setae; second article 0.6 times as long as first with outer distal tuft of setae; third article just shorter than second; distal article very small, with eight distal setae and three aesthetascs.

Antenna (Fig. 10E) of six articles, first article naked, one-quarter length of second; second article with slight dorsal flange-like expansion and ventrodistal tuft of three setae; third article half length of second, with smaller dorsal flange-

like expansion; fourth article longest, 1.5 times as long as second article; fifth article 0.6 times as long as fourth; sixth article very small with eight distal setae.

Labrum (Fig. 10G) extended centrally, rounded, setose. Left mandible (Fig. 10H) with wide, robust, distally denticulate lacinia mobilis, right mandible (Fig. 10I) with narrower, distally crenulate lacinia mobilis; pars molaris of each mandible robust, rugose. Labium (Fig. 10J) wide, all lobes finely setose distally, labial palp absent. Maxillule (Fig. 10K) with seven distal spines, finely setose outer margin, palp with two distal setae. Maxilliped (Fig. 10L) typical of genus, basis with single seta reaching proximal margin of palp article 2; proximal palp article naked, second palp article with outer seta four simple inner setae; third article with five plumose and three simple inner setae in two rows; fourth article with one inner, three distal and two outer subdistal simple setae. Maxilliped endites (Fig. 10M) with one simple and one longer coarsely-plumose setae, the latter reaching proximal margin of fourth palp article. Epignath (Fig. 10N) typical of genus, elongate with distal spine and finely setose distal margin.

Cheliped (Fig. 11A) comparatively stout, basis 1.16 times as long as wide with ventrodistal seta; merus ventrally with single subdistal seta; carpus as long as wide, with single dorsodistal paired midventral setae; propodus with single ventral seta, fixed finger with outer distal tubercle bearing four setae, two inner distal setae, cutting edge distally expanded into squared
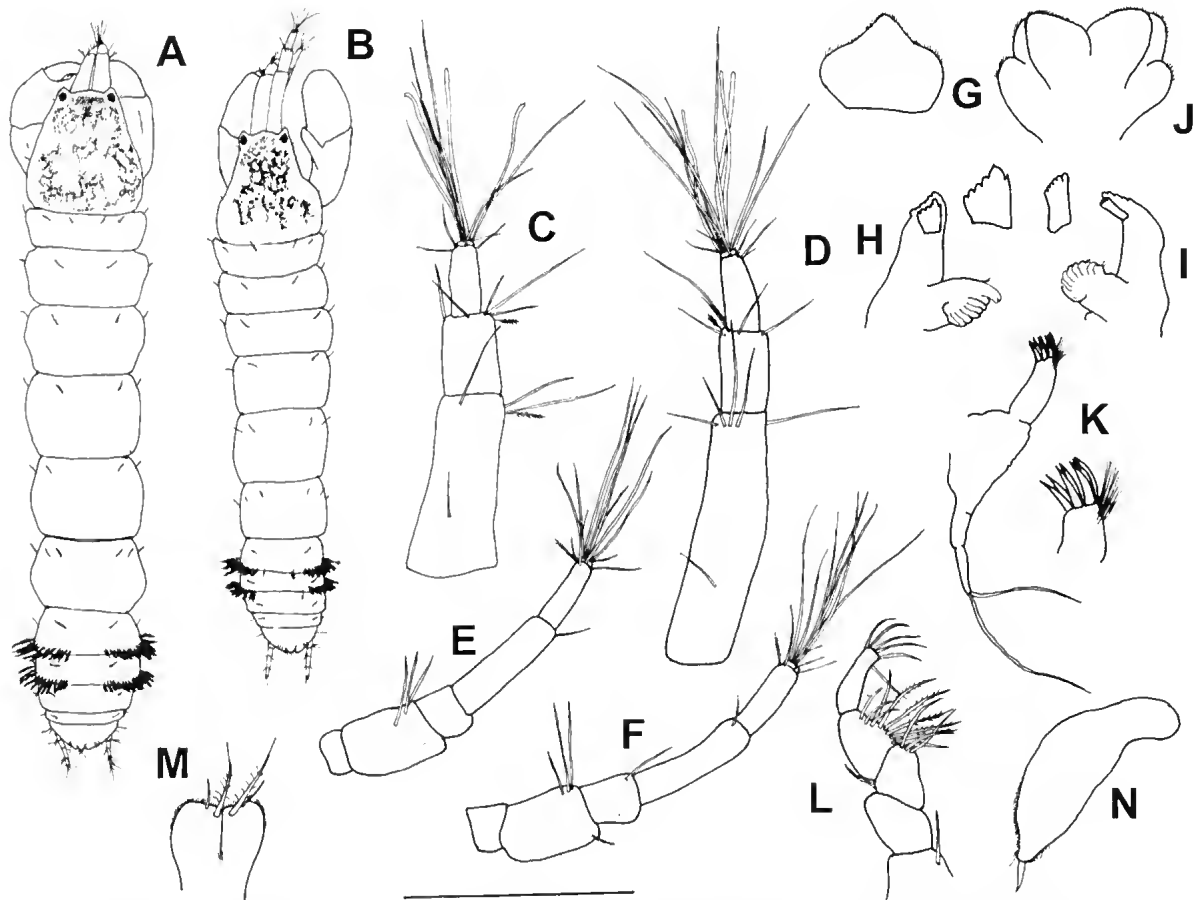
FIG. 10. *Sinelobus pinkenba* sp. nov., **A**, female holotype, dorsal; **B**, male, dorsal; **C**, female antennule; **D**, male antennule; **E**, female antenna; **F**, male antenna; **G**, labrum; **H**, left mandible; **I**, right mandible; **J**, labium; **K**, maxillule; **L**, maxilliped; **M**, maxilliped endites; **N**, epignath; Scale bar = 1.5 mm for A, B; 0.4 mm for C–N.
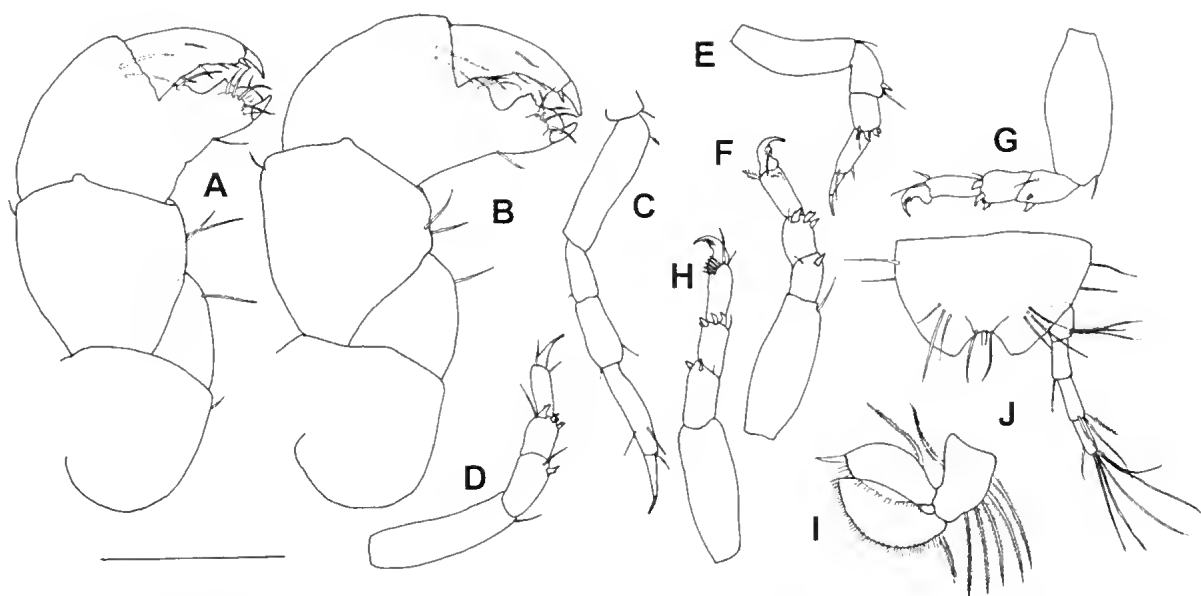
FIG. 11. *Sinelobus pinkenba* sp. nov., **A**, female cheliped; **B**, male cheliped; **C–H**, pereopods 1–6; **I**, pleopod (most setae shown only by their bases); **J**, pleotelson and right uropod. Scale bar = 0.4 mm for A–H, 0.3 mm for I, J.

lamella; dactylus with four fine setae submarginally along cutting edge and simple spine adjacent to claw.

Pereopod 1 (Fig. 11C) longer than others, with sparse simple setae as figured; coxa with seta but no apophysis; basis slender, 3.8 times as long as wide; ischium fused; merus 0.4 times length of basis; carpus one-third longer than merus; propodus 1.5 times as long as carpus; dactylus with distinct, slender, shorter claw, both together 0.6 times as long as propodus. Pereopod 2 (Fig. 11D) basis 3.7 times as long as wide with ventrodistal seta; merus half length of basis with ventrodistal seta and short tooth-like spine; carpus compact, shorter than merus, with dorsal seta, three anteroventral and two posteroventral short tooth-like spines; propodus 1.3 times as long as carpus; dactylus plus claw as long as carpus. Pereopod 3 (Fig. 11E) similar to pereopod 2 but smaller.

Pereopod 4 (Fig. 11F) basis 2.25 times as long as wide, with single ventrodistal seta; merus 1.1 times as long as carpus, with paired subdistal ventral short spines, carpus with crown three anteroventral and two posteroventral short tooth-like spines, each spine with subdistal seta; propodus 1.2 times as long as merus; dactylus and

unguis fused into a claw, curved, with lateral comb of six or seven spinules. Pereopod 5 (Fig. 11G) as pereopod 4. Pereopod 6 (Fig. 11H) as pereopod 4, but propodus with distal row of five leaf-like spines.

Pleopod (Fig. 11I) basis with single inner plumose seta and five outer plumose setae; exopod with numerous plumose setae along outer edge; endopod with one inner proximal and ten outer plumose setae, distally with shorter, stout, articulate seta.

Uropod (Fig. 11J) uniramous, of three segments plus basis, segments 2–3 times as long as wide, subequal in length; basis with conspicuous outer-distal tuft of three setae.

Distinctions of male: body (Fig. 10B) similar to but smaller than female (figured specimen 3.3 mm long), cephalothorax with concave anterior lateral margins. Pereonites comparatively shorter, pereonites 2 and 3 being 1.2 times as long as pereonite 1.

Antennule (Fig. 10D) proportionately longer, proximal article 3.9 times as long as wide. Antenna (Fig. 10F) slightly more slender, article 2 and 3 with more pronounced dorsal flange-like expansions.

Cheliped (Fig. 11B) proportionately larger and more robust, although ornamentation of chela identical.

Etymology. Pinkenba is the district of Brisbane in which lies Bulwer Island, where the type material was found.

Remarks. *Sinelobus staufordi* (Richardson, 1901) is a brackish water species which has been regarded as cosmopolitan in the tropics and subtropics in lagoons and estuaries since Lang (1956) and subsequently Sieg (1980) synony-mised all described species of the genus. Previous Australian records of this species are from Queensland, from the Ross River near Townsville and the Mowbray River near Hockley (Sieg 1980). Edgar (2008), while describing as new *S. barretti*, the first distinguished species of *Sinelobus* from Australian waters, quite rightly pointed out the unlikelihood of all the known records, from a global distribution and a range of habitats, being of a single species. Those previous records from Queensland may in fact be of the present species.

In distinction from *Sinelobus staufordi sens. auctt.*, *S. pinkenba* sp. nov. shows similarities only to the Tasmanian *S. barretti* in a reduced sexual dimorphism of the cheliped (carpus with-out ventral tubercles; chela fingers shorter), in having seven distal spines on the maxillule (also found in '*S. staufordi*' sensu Shiino, 1965) and a less-slender proximal antennule article. The present species differs from *S. barretti* in the proportions of the uropod segments, in the distal position of the seta-bearing tubercle on the chela fixed finger (proximal in *S. barretti*), in the setation of the mouthparts, and from this and all other described forms of *Sinelobus* in the flange-like expansions on the second and third articles of the antenna.

It is possible that the low degree of sexual dimorphism shown by the present species is because the males are not fully mature.

Subfamily Pancolinae Sieg, 1980
Tribe Anatanaini Sieg, 1980

Zeuxo Templeton, 1840

Zeuxo (Parazeuxo) amiti **sp. nov.**
(Figs 12, 13)

Material Examined. HOLOTYPE: QM-W28088, ♀, amongst *Cladophoropsis vaucheriaeformis*, Amity Point, North Stradbroke I., 27°23.9′S, 153°26.2′E, 0.5 m, 20.02.2005. PARATYPE: QM-W28089, ♀ with oostegites, dissected amongst sponges, Shag Rock, north of North Stradbroke I., 27°24.8′S, 153°31.5′E, 15 m, 15.02.2005, both A-NL.

Description. Female typical *Zeuxo*, body (Fig. 12A) slender, dorsally with black mottling on cephalon, pereonites and pleonites, darkest as bar between eyes; length of holotype 1.75 mm. Cephalothorax subrectangular, 1.1 times as wide as long, with slight rounded frons but no rostrum, eyes present, pigmented. Cephalothorax shorter than pereonites 1–3 together. Six free pereo-nites, rounded laterally, with one or two small lateral setae on each side and paired dorso-lateral setae towards anterior of pereonite; pereo-nite 1 shortest, two-thirds as long as pereonite 2, pereonite 3 longer than pereonite 2, pereonite 4 1.7 times as long as pereonite 1, pereonite 5 longest, 2.6 times as long as pereonite 1, pereonite 6 twice as long as pereonite 1 (all pereonites respectively 3.6, 2.4, 2.1, 1.6, 1.4 and 1.8 times as wide as long). Pleon of five free pleonites with lateral seta on each side, paired dorsolateral setae on pleonites 1–4 only; pleonite 1 three times as wide as long, pereonites 2 and 3 sub-equal, shorter, 4.5 times as wide as long, with-out transverse dorsal rows of setae, bearing pleopods; pleonites 4 and 5 shorter and narrower, 6 times as wide as long, without pleopods. Pleo-telson subpentangular, 1.6 times as wide as long, distally bifurcate, with single lateral and dorso-lateral setae on each side and paired distal setae.

Antennule (Fig. 12B) of four articles, proxi-mal article twice as long as wide, with two longer distal simple setae and one plumose sensory seta; second article half as long as first with distal crown of four setae; third article two-thirds as long as second with two distal setae; distal article very small, with four distal setae and four aesthetascs.

Antenna (Fig. 12C) of seven articles, first and third articles subequal, naked, half length of second; second, fourth and fifth articles sub-equal, setose as figured; sixth and seventh articles very small with five and four distal setae respectively.

Labrum rounded, setose. Left mandible (Fig. 12D) with small, rounded lacinia mobilis, right
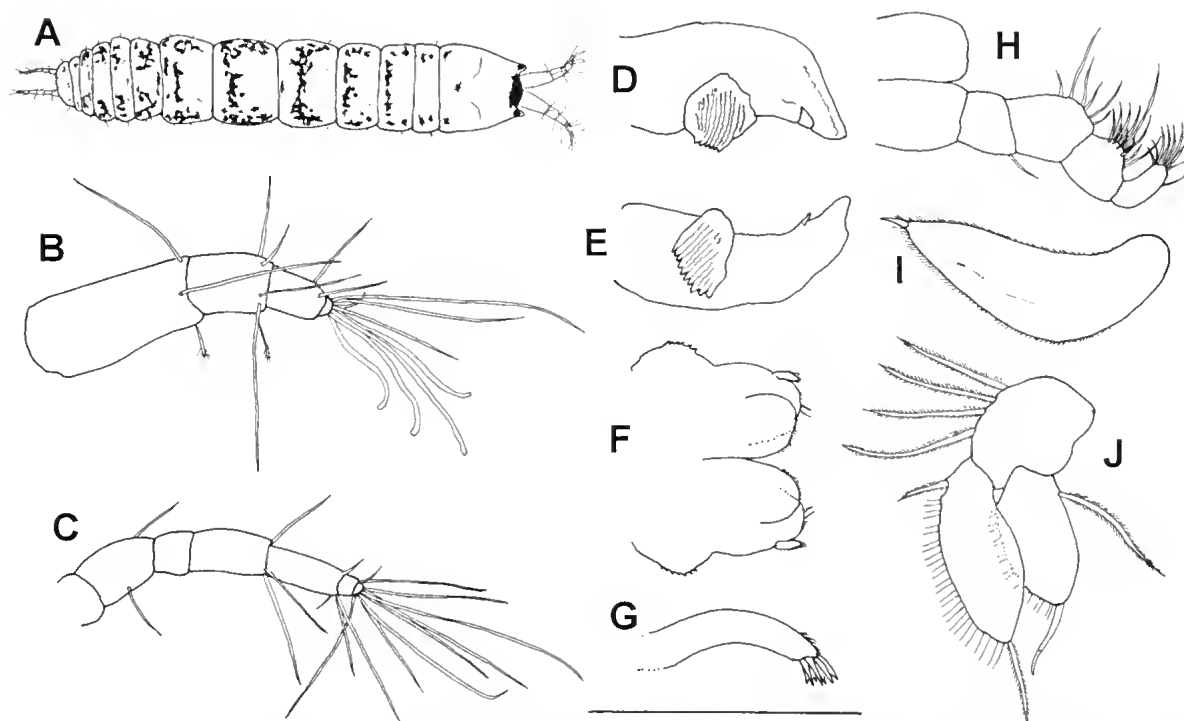
FIG. 12. *Zeuxo amiti* sp. nov., **A**, holotype, dorsal; **B**, antennule; **C**, antenna; **D**, left mandible; **E**, right mandible; **F**, labium; **G**, maxillule endite; **H**, maxilliped; **I**, epignath; **J**, pleopod (most setae shown only by their bases). Scale bar = 1 mm for A; 0.2 mm for B–J.

mandible (Fig. 12E) with minute, scale-like lacinia mobilis; pars molaris of each mandible robust, rugose. Labium (Fig. 12F) inner lobe finely setose distally, outer lobe with midlateral denticulations, labial palp present, finely setose. Maxillule (Fig. 12G) with eight distal spines, finely setose outer margin, palp not seen. Maxilliped typical of genus, proximal palp article only with outer seta (Fig. 12H). Epignath (Fig. 12I) typical of genus, elongate with distal spine and finely setose margin.

Cheliped (Fig. 13A) comparatively stout, basis 1.45 times as long as wide with ventrodistal seta; merus ventrally with paired subdistal setae; carpus 1.6 times as long as wide, dorsally with single proximal and two distal setae, ventrally with three subdistal setae; propodus with three ventral setae, fixed finger with crown of six setae, cutting edge smooth; dactylus with row of fine setae submarginally along cutting edge.

Pereopod 1 (Fig. 13B) longer than others, with sparse simple setae as figured; coxa with seta but no apophysis; basis slender, 4.7 times as long as wide; ischium fused; merus one-third length of basis; carpus one-third longer than merus; propodus 1.5 times as long as carpus; dactylus with distinct, slender, longer claw, both together 0.85 times as long as propodus. Pereopod 2 (Fig. 13C) basis 3.6 times as long as wide; merus half length of basis with paired ventrodistal short spines; carpus compact, shorter than merus, with two dorsal, two anteroventral and two posteroventral spines; propodus 1.6 times as long as carpus; dactylus plus claw just longer than carpus. Pereopod 3 (Fig. 13D) similar to pereopod 2, but basis shorter, no ventrodistal seta on carpus.

Pereopod 4 (Fig. 13E) basis 2.3 times as long as wide, with two distal setae and single ventral plumose sensory seta; merus 1.3 times as long as carpus, with paired subdistal ventral spines, carpus with crown of six distal spines, each spine with subdistal seta; propodus just longer than merus; dactylus and unguis fused into a claw, curved, with lateral comb of 4 spinules. Pereopod 5 (Fig. 13F) as pereopod 4. Pereopod
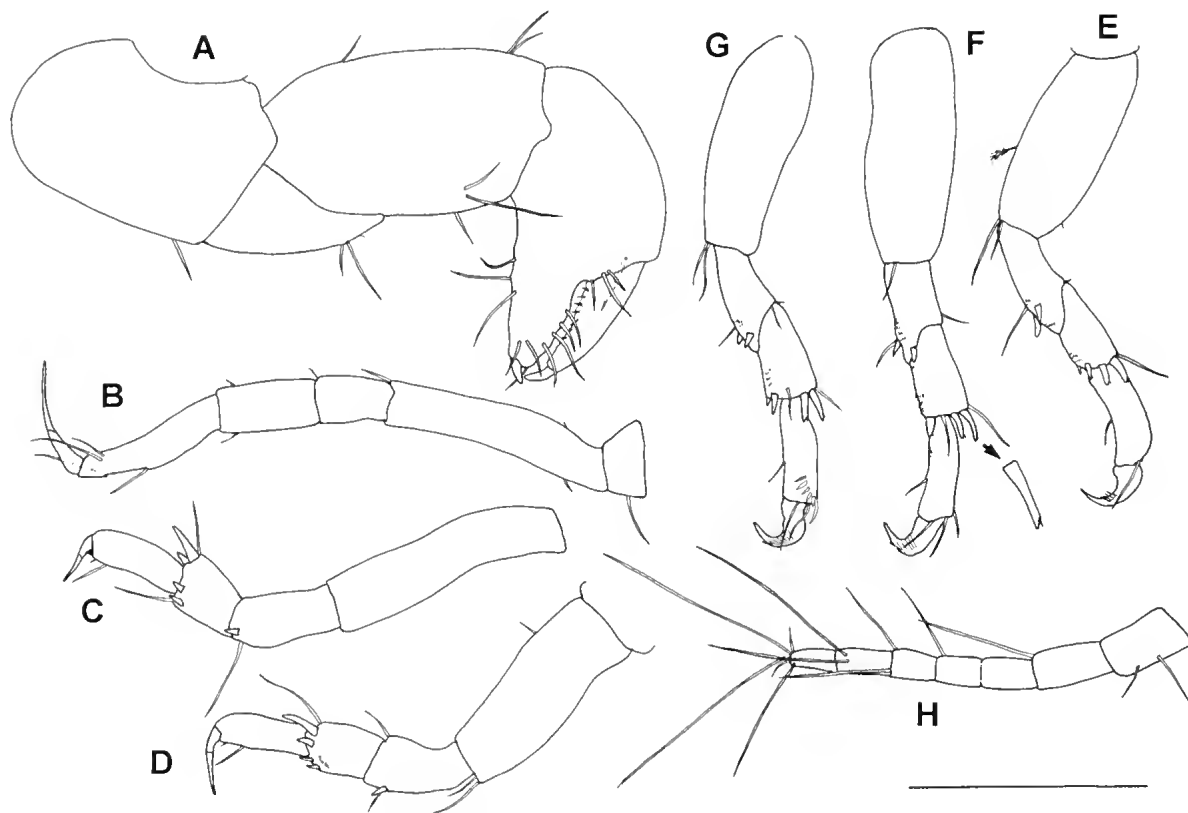
FIG. 13. *Zeuxo amiti* sp. nov., **A**, cheliped; **B-G**, pereopods 1–6; H, uropod. Scale bar = 0.2 mm.

6 (Fig. 13G) as pereopod 4, but propodus with distal row of five leaf-like spines.

Pleopod (Fig. 12J) basis with naked inner margin and four outer plumose setae; exopod with 15 plumose setae along outer edge; endopod with one inner and ten outer plumose setae, distally with shorter, stout, articulate seta.

Uropod (Fig. 13H) uniramous, of six segments plus basis, segments 2–3 times as long as wide, subequal in length.

Male unknown.

Etymology. From *Amity* Point, on the north-west coast of South Stradbroke I., where the holotype was found.

Remarks. The genera within the Anataini, *Anatanais* Nordenstam, 1930, *Zeuxo*, and *Zeuxoides* Sieg 1980, are poorly distinguished, Sieg (1980), for example, relying on the proportions of the proximal antennular article as a major distinction, even though this does show intraspecific variation in some of the taxa (G. Bird, pers.

comm.). The short antennular peduncle article of *Zeuxo amiti* sp. nov. would imply its being a species of *Anatanais*, yet the total lack of a coxal apophysis on pereopod 1, the reduction of the lacinia mobilis on both mandibles, the sparse setation of the pleopod bases, and the proportionate length of the uropod articles all preclude it from that genus. Despite the antennular proportions, the present species is consistent with the subgeneric diagnosis of Stock (1980) for *Parazeuxo*, a taxon which does include species with underdeveloped coxal apophyses on pereopod 1, a reduced mandibular lacinia mobilis, four antennular aesthetascs in the female and reduced pleopod setation (notably only a single seta on the inner margin of the pleopod endopod).

Edgar (2008) described six new species of *Zeuxo* from Australian waters, three of which, *Z. belli*, *Z. mooneyi* and *Z. russi*, are attributable to the subgenus *Parazeuxo*. *Z. mooneyi* has a compact four-segmented uropod and a broad, crenulated lacinia mobilis on the left mandible.

Both of the other species have seven-segmented uropods in the adult and a relatively compact antennule, but, unlike Z. *amiti*, they have a distinct coxal apophysis on pereopod 1, more numerous ventral setae on the cheliped fixed finger, better-developed rows of leaf-like spines on the propodus of pereopod 6, and a distinct dorsal pigmentation. All three of these species have a single seta on the inner margin and more than four setae on the outer margin of the pleopod basis, unlike Z. *amiti*.

Zeuxo amiti is distinct from all other described members of the subgenus in its compact antennule. The only other described species of *Zeuxo (Parazeuxo)* with a single seta on the inner margin of the pleopod endopod and more than five articles in the uropod (>4 segments plus basis) are Z. *(P.) seurati* (Nobili, 1906) from Tuamotu and Hawaii (incl. *Anatanais insularis* Miller, 1940), and Z. *(P.) cloacarattus* Bamber, 2006, from New Caledonia. Those species also have a reduced lacinia mobilis on each mandible, but their antennular proximal peduncle articles are 2.6 and 3 times as long as wide respectively, their chelipeds are more compact (carpus respectively 1.5 and 1.4 times as long as wide), and they both have a coxal apophysis on pereopod 1 (Sieg 1980; Bamber 2006).

Superfamily Paratanaoidea Lang, 1949

Family Anarthruridae Lang, 1971
Subfamily Leptognathiinae Sieg, 1976

Tanaopsis Sars, 1896

Tanaopsis canaipa sp. nov.
(Figs 14, 15)

Material Examined. HOLOTYPE: QM-W28165, ♀, without oostegites, ♀, dissected, MBWS Stn. 15E, Moreton Bay. PJFD. PARATYPE: QM-W28166, ♀ without oostegites, Middle Banks, northern Moreton Bay, 17.09.1983/13.01.1984, P. Saenger & S. Cook (there are two dates on the label, in material that contained a number of species).

Description. Female body (Fig. 14A) attenuate, length of holotype 4 mm, 8.75 times as long as wide. Cephalothorax subrectangular, 1.33 times as wide as long, with slight rostrum; single midlateral setae. Eyelobes and eyes absent.

Six free rectangular pereonites with single midlateral setae. Pereonite 1 shortest, one third

as long as cephalon and 2.2 times as wide as long; pereonites 2 and 3 subequal, 1.5 times as long as pereonite 1, 1.4 times as wide as long; pereonites 4 and 5 longest, subequal, 2.5 times as long as pereonite 1, 1.1 times as long as wide; pereonite 6 shorter, twice as long as pereonite 1, 1.2 times as wide as long. Pleon wide than pereon, of five free pleonites, subequal but progressively shorter posteriorly, each about 3.2 times as wide as long; pleopods on all pleonites. Pleotelson semicircular, 1.75 times as wide as long, distally extended, with two distal setae.

Antennule (Fig. 14B) of four articles, proximal peduncle article twice as long as wide, distally with one longer outer and one shorter inner setae and two pinnate sensory setae on outer margin; second article 0.43 times as long as first with long outer subdistal seta, 1.5 times as long as article; third article 0.43 times as long as second with single inner and outer simple distal setae; distal article (flagellum) as long as proximal peduncle article, with one longer and four shorter distal setae and single aesthetasc.

Antenna (Fig. 14C) of six articles, setose as figured, first three articles compact, fourth article longest, three times as long as second and 3.8 times as long as wide, fifth article as long as second, sixth article tiny with six distal setae.

Labrum rounded, naked. Right mandible (Fig. 14E) relatively simple, pars incisiva with crenulated egde, pars molaris a simple process; left mandible (Fig. 14F) similar but with delicate pars incisiva. Labium (Fig. 14D) of two wide, naked lobes without palp. Maxillule (Fig. 14G) with six shorter and one more robust distal spines, outer margin with tufts of fine setules; palp of two articles with two distal setae. Maxilla and epignath not seen. Maxilliped (Fig. 14H) endites distally with rounded lateral lobes, single inner distal seta; maxilliped basis fused medially, with single long distal seta not reaching distal margin of epignath; palp first article naked, second and third articles each with two inner simple setae; fourth article with five distal simple setae.

Cheliped (Fig. 15A) basis 1.8 times as long as wide, naked; merus triangular, with single ventral seta; carpus 1.5 times as long as wide with two ventral marginal setae and one middorsal and one dorsodistal setae; chela as long as carpus;
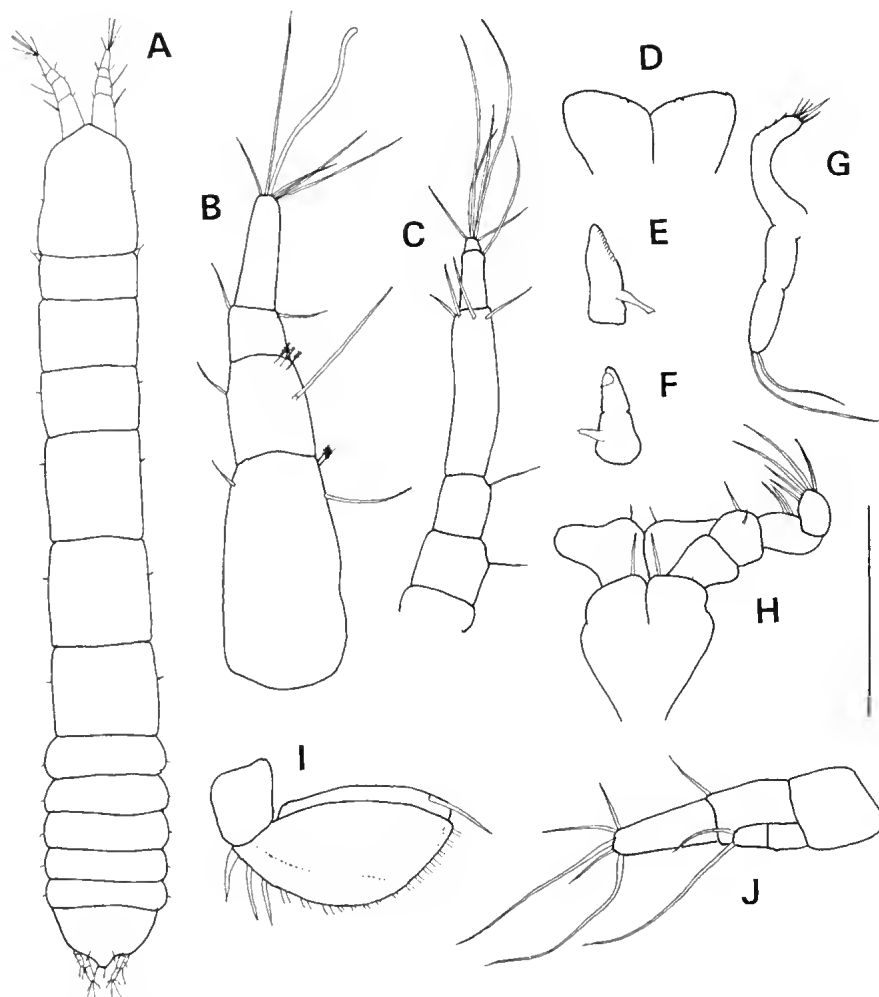
FIG. 14. *Tanaopsis canaipa* sp. nov., **A**, holotype female, dorsal; **B**, antennule; **C**, antenna; **D**, labium; **E**, right mandible; **F**, left mandible; **G**, maxillule; **H**, maxilliped; **I**, pleopod (most setae shown only by their bases); **J**, uropod. Scale bar = 0.5 mm for A; 0.1 mm for B–J.

propodus with distal comb of three shorter and one longer setae at base of dactylus, fixed finger with two ventral setae, one distal seta and two setae distally on cutting edge, distally with inner bifurcate claw and outer trifurcate claw between which claw of dactylus sits; fingers of chela shorter than palm; dactylus with simple cutting edge but corrugated dorsal margin typical for genus.

Pereopod 1 (Fig. 15B) much longer than others; coxa with triangular apophysis bearing simple seta; basis slender, four times as long as wide, naked; ischium with single ventral seta; merus and carpus subequal, 0.3 times as long as basis; merus naked, carpus with small, single ventro-distal and dorsodistal setae; propodus longer than merus and carpus together, tapering, dorsally with subdistal group of three setae, single ventrodistal seta and longer distal seta exceeding tip of dactylus; dactylus with small distal seta, slender unguis twice length of dactylus, both together 1.34 times as long as propodus. Pereopod 2 (Fig. 15C) similar to but smaller than pereopod 1, coxa with simple seta but without apophysis, merus shorter than carpus, propodus not tapering with ventrodistal seta longer than dactylus. Pereopod 3 (Fig. 15D) similar to pereopod 2, but propodus with two subdistal dorsal setae, dactylus and unguis together just as long as propodus.
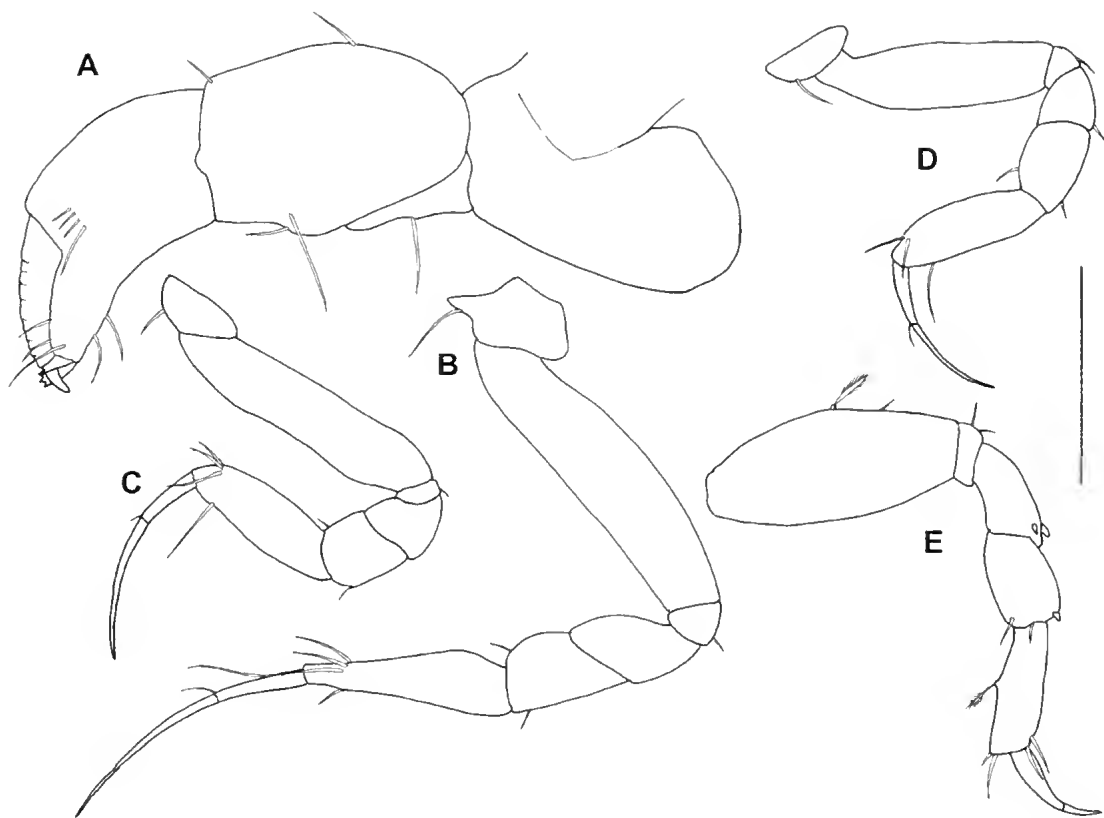
FIG. 15. *Tanaopsis canaipa* sp. nov., **A**, cheliped; **B–E**, pereopods 1, 2, 3 and 5 respectively. Scale bar = 0.13 mm for A; 0.1 mm for B–E.

Pereopods 4, 5 (Fig. 15E) and 6, similar to each other; basis stouter, twice as long as wide, with midventral pinnate sensory seta; ischium with two ventral setae; merus shorter than carpus, merus with two and carpus with one ventro-distal tooth-like spines, carpus with two simple dorsodistal setae; propodus with three distal setae (four on pereopod 6); dactylus and unguis not fused but forming curved claw shorter than propodus.

Pleopod (Fig. 14I) basis naked; exopod with 18 plumose setae along outer edge; endopod with one distomedial plumose seta and nine plumose setae around distal margin.

Uropod (Fig. 14J) biramous, basis naked, exopod just shorter than proximal segment of endopod, of two segments, proximal segment with outer distal seta, distal segment with two distal setae of which outer is far longer; endopod of two segments, proximal segment with shorter inner and onger outer distal setae, second segment with five distal setae.

Male unknown.

Etymology. 'Canaipa' is a local Aboriginal name for a passage along the southwest of North Stradbroke Island in Moreton Bay.

Remarks. Sieg & Dojiri (1991) presented a key to the species of *Tanaopsis* as then known. To these must be added *Tanaopsis gallardoi* (Shiino, 1970) (moved from *Leptognathia* by Bird & Bamber, 2000) and *T. chotkarakde* Bird & Bamber, 2000. *T. canaipa* sp. nov. is remarkably attenuate for the genus, with pereonites 4 and 5 longer than wide. The only other species so attenuate is *T. antarctica* Lang, 1967, which is distinct from the present species in a number of features, including having the distal seta on the maxilliped basis exceeding the tip of the endites, more numerous setae on the maxilliped palp articles, a shorter proximal antennule article, a cheliped

with a more compact basis and carpus (1.3 times as long as wide), no distal setae on the dactyli of the pereopods, and more setae on the pleopods.

Subfamily Akanthophoreinae Sieg, 1986

Tangalooma gen. nov.

Diagnosis. Small, compact tanaidomorph, dorsoventrally flattened; cephalon with rostrum, eyelobes and eyes; antennule of four articles in the female, that of the male of eight articles (including minute distal article) bearing numerous aesthetascs; antenna of six articles without dorsal or ventral spines on articles 2 and 3. In female, mandible with robust pars molaris, lacinia mobilis absent; maxillule with six distal spines; mouthparts of male atrophied. Chelipeds highly dimorphic, that of male more robust, the chela almost subchelate. Pereopods 1 and 2 ambulatory, dactylus and unguis not fused; pereopod 3 of female reduced, ambulatory; pereopods 4–6 of female with fused and compound claw; all pereopods of male ambulatory, although carpus endowed with distal tooth-like spines. Five free pleonites without plumose lateral setae, all bearing biramous pleopods. Uropods biramous, exopod of one segment, endopod of two segments.

Type species: *Tangalooma rous* sp. nov., by original designation.

Etymology. 'Tangalooma' is the local Ngugi Aboriginal name of a settlement on Moreton Island.

Tangalooma rous sp. nov.
(Figs 16, 17)

Material Examined. HOLOTYPE: QM-W28090, ♀ without oostegites, QM-W28091, ♂, allotype, on the bryozoan *Orthoscuticella ventricosa* aggregate, Henderson's Pinnacles, east side of Moreton I., 27°07.901'S, 153°28.712'E, 22–26m, 22.02.2005, A-NL.

Description of female (based on anatomy examined *in situ*): body (Fig. 16A) compact, small, length of holotype 0.75 mm. Cephalothorax subrectangular, 1.1 times as wide as long, with prominent, rounded rostrum; single lateral seta behind eyelobe and paired lateral setae in posterior half. Eyelobes present, eyes with black ocelli.

Six free pereonites, anterior three pointed laterally with one or two simple lateral setae, posterior three rounded laterally, naked. Pereonites 1 and 2 shortest, 7–8 times as wide as long; pereonite 3 1.4 times as long as pereonite 2, four times as wide as long; pereonites 4 and 6 subequal, twice as long as pereonite 1, about three times as wide as long; pereonite 5 longest, three times as long as pereonite 2, twice as wide as long. Pleon of five free pleonites, subequal but progressively shorter posteriorly, about seven times as wide as long; pleopods on all pleonites. Pleotelson semicircular, twice as wide as long, distally entire, with two distal setae.

Antennule (Fig. 16C) of four articles, proximal peduncle article 1.5 times as long as wide, distally with one longer simple seta and two pinnate sensory setae on outer margin; second article 0.6 times as long as first with two outer distal setae, the longer exceeding distal tip of antennule; third article 0.7 times as long as second with single inner and outer simple distal setae; distal article (flagellum) as long as second peduncle article, with one longer and three shorter distal setae and single aesthetasc.

Antenna (Fig. 16E) of six articles, setose as figured, first three articles compact, fourth article longest, three times as long as third and three times as long as wide, fifth article half as long as fourth, sixth article tiny with four distal setae.

Labrum (Fig. 16G) rounded, hood-like, marginally finely setose. Left mandible (Fig. 16K) relatively simple, with slender, bifurcate pars incisiva and stout pars molaris with one slender and numerous rounded marginal teeth; right mandible (Fig. 16J) much as left mandible but pars incisiva wider. Labium (Fig. 16H) of two simple, naked lobes without palp. Maxillule (Fig. 16I) with six distal spines and single outer distal seta. Maxilla and epignath not seen. Maxilliped endites apparently distally simple, naked; maxilliped basis not fused, with single long distal seta; palp (Fig. 16L) first article naked, second with four distal simple setae and possibly one fine outer seta; third article with inner group of four longer simple setae and shorter adjacent dorsal seta; fourth article with six distal simple setae.

Cheliped (Fig. 17A) with comparatively stout basis just longer than wide, naked; merus triangular, with single ventral seta; carpus twice as long as wide with three ventral marginal setae and one dorsodistal seta; chela as long as carpus;
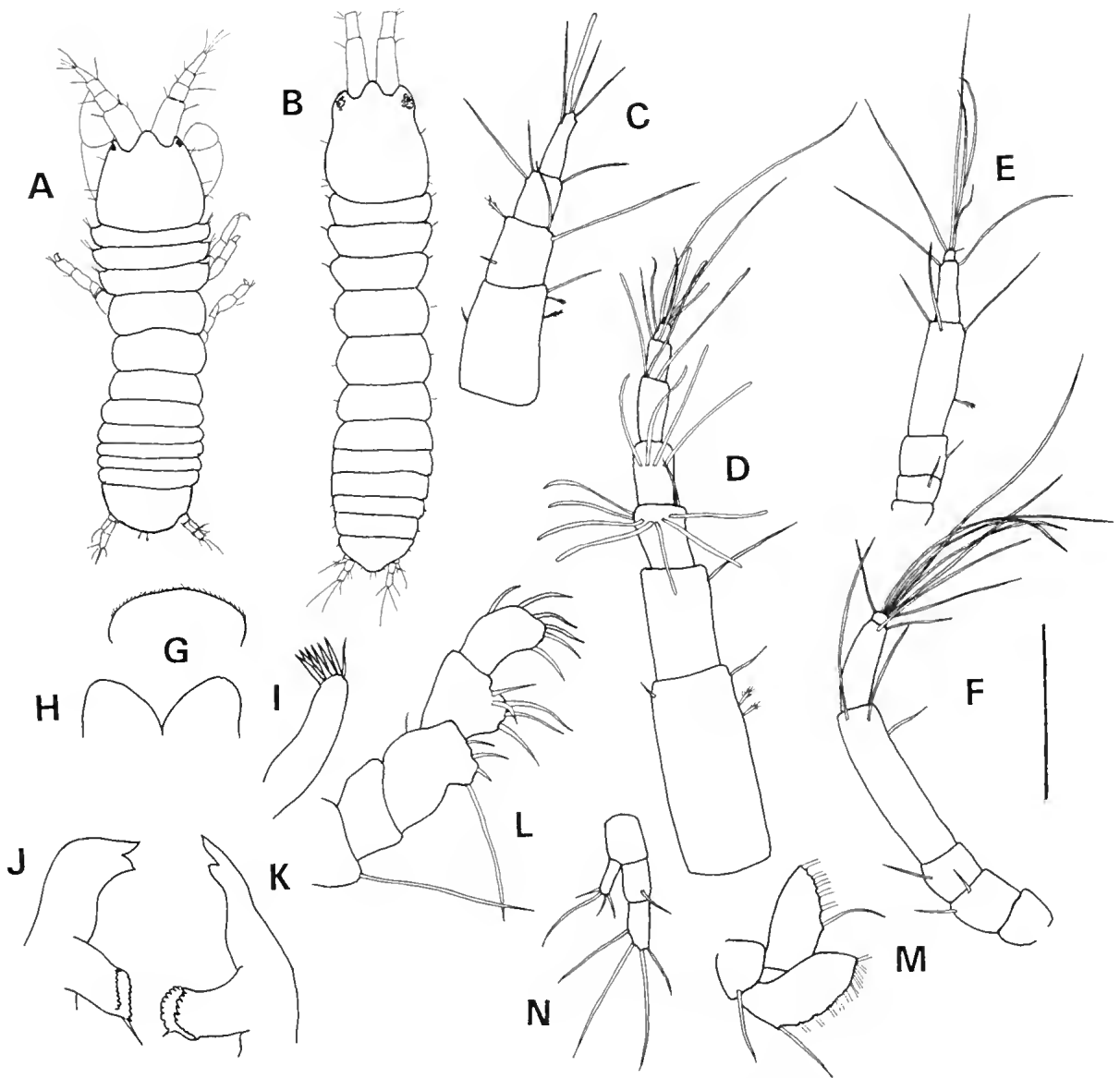
FIG. 16. *Tangalooma rous* gen. et sp. nov., **A**, female holotype; **B**, male allotype; **C**, female antennule; **D**, male antennule; **E**, female antenna; **F**, male antenna; **G**, labrum; **H**, labium; **I**, maxillule; **J**, right mandible; **K**, left mandible; **L**, maxilliped; **M**, third pleopod; **N**, uropod. Scale bar = 0.3 mm for A, B; 0.1 mm for C–N.

propodus twice as long as wide with one mid-ventral, one inner and paired dorsal setae on fixed finger; fingers of chela shorter than palm (propodus); dactylus with simple cutting edge and simple proximal inner seta.

Pereopod 1 (Fig. 17D) longer than others; coxa without apophysis; basis slender, five times as long as wide; ischium naked; merus and carpus subequal, twice as long as wide and 0.4 times as long as basis; merus with paired ventrodistal setae, carpus with single ventrodistal seta and longer dorsodistal seta longer than article; pro-podus twice as long as carpus with subdistal crown of four simple setae; dactylus naked, shorter than distinct, slender unguis, both together two-thirds as long as propodus. Pereopod 2 (Fig. 17E) similar to pereopod 1, coxa with long simple seta, ischium with ventrodistal seta, merus
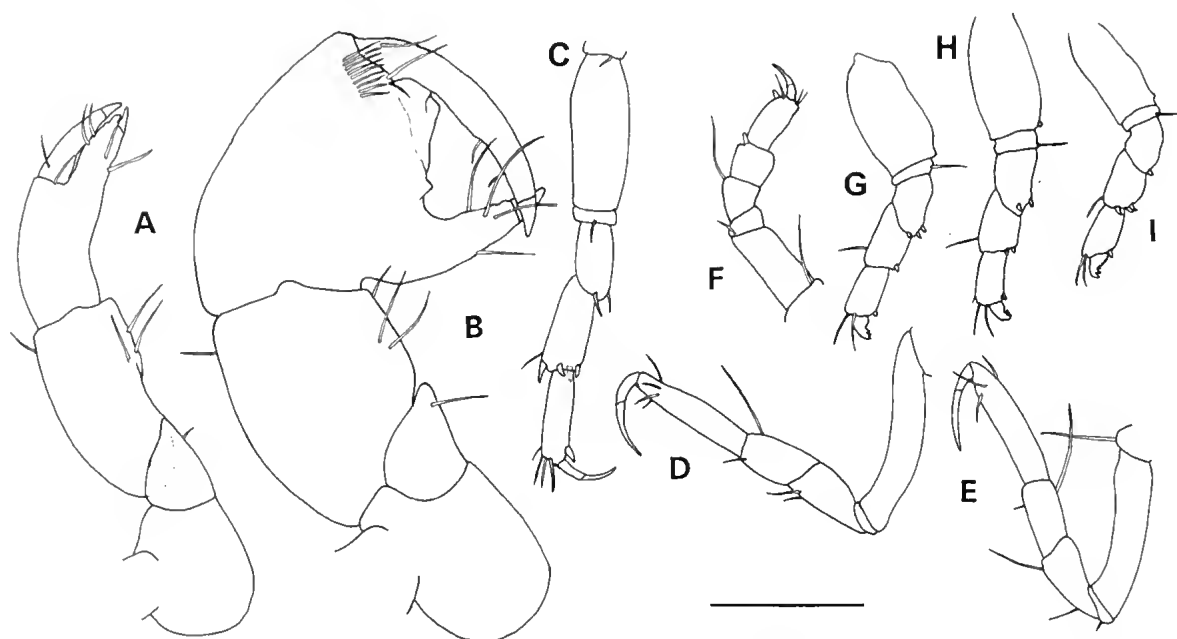
FIG. 17. *Tangalooma rous* gen. et sp. nov., **A**, cheliped of female; **B**, cheliped of male; **C**, pereopod 5 of male; **D–I**, pereopods 1–6 of female. Scale bar = 0.1 mm.

with single, longer ventrodistal seta. Pereopod 3 (Fig. 17F) more compact than pereopod 2, basis about twice as long as wide, merus and carpus as long as wide; merus with slender ventrodistal seta, carpus small, stout ventrodistal spine; propodus twice as long as wide, with small, stout ventrodistal spine; dactylus and unguis distinct, together 0.7 times as long as propodus.

Pereopod 4 (Fig. 17G) basis stout, twice as long as wide, naked; ischium short with ventrodistal seta; merus, carpus and propodus subequal; merus and carpus each with two ventrodistal tooth-like spines, carpus with simple dorsodistal seta; propodus with single ventrodistal tooth-like spine and two dorsodistal setae; dactylus and unguis fused into short claw, curved, with three ventral denticulations. Pereopod 5 (Fig. 17H) as pereopod 4. Pereopod 6 (Fig. 17I) as pereopod 4, but carpus with three tooth-like spines, claw with four denticulations.

Pleopod (Fig. 16M) basis with single ventrodistal plumose seta; exopod with ten plumose setae along outer edge; endopod with six plumose setae around distal margin.

Uropod (Fig. 16N) biramous, basis naked, exopod of one segment with three short and one longer distal setae, endopod of two segments (articulation obscure), first segment with single mesial and distal inner setae, second segment with one subdistal and three distal setae.

Description of male: generally similar to but larger than female, showing dimorphism of antennule, mouthparts, cheliped and posterior pereopods. Body (Fig. 16B) more elongate; length of allotype 0.92 mm. Cephalothorax 1.1 times as long as wide. Pereonites 1–3 longer than in female (five, three and three times as wide as long respectively). Pleonites longer than in female, about four times as wide as long.

Antennule (Fig. 16D) of eight articles, proximal peduncle article 2.5 times as long as wide; second article 0.6 times as long as first; distal articles progressively thinner, third to seventh articles with seven, four, three, one and one distal aesthetascs respectively; distal article tiny, anaxial. Antenna (Fig. 16F) similar to that of female, distal article with six distal setae.

Mouthparts entirely atrophied.

Cheliped (Fig. 17B) robust, carpus 1.25 times as long as wide; propodus slightly wider than long, almost triangular, fixed finger originating from entire ventral margin, distal margin with outer membranous extension and row of nine

setae at base of dactylus; dactylus plus unguis twice as long as fixed finger.

Pereopods 1 and 2 similar to those of female, but carpus longer than merus. Pereopod 3 similar to pereopod 2. Pereopods 4–6 (e.g. Fig. 17C) more slender than those of female, with paired ventrodistal setae on ischium and merus; carpus with single dorsodistal and three ventrodistal tooth-like spines; dactylus and unguis not fused, two-thirds as long as propodus.

Pleopods and uropods as those of female.

Etymology. 'Rous' is a local Australian Aboriginal name of a channel next to Chain Banks in Moreton Bay.

Remarks. The unique combination of extreme sexual dimorphism in the cheliped, modified pereopod 3 in the female, compound claw on the posterior pereopods in the female, short uropod and atrophied male mouthparts justify erection of a new genus for this species, but make the attribution of this species to a supra-generic taxon somewhat difficult. While there are some similarities with *Armaturatanais* Larsen, 2005 (*q.v.*) in terms of the gross morphology, the antennular, antennal and mouthpart morphology, any such association is precluded by the fused claws of the posterior pereopods and the high degree of sexual dimorphism. The four-articled female antennule, distal aesthetascs, short uropod, lack of plumose lateral setae on the pleonites and modified female posterior pereopods are variously inappropriate to Leptocheliidae, Pseudotanaidae, Paratanaidae, Typhlotanaidae, Pseudozeuxidae and Nototanaidae. Within the Anarthruridae, the robust molar process of the mandible is characteristic of the Akanthophoreinae, wherein there are already a few 'aberrant' genera, *Cristatotanais* Kudinova-Pasternak, 1990, for example, showing fusion of the dactylus and unguis of the posterior pereopods.

The dimorphism of the posterior pereopods is attributed to the female showing adaptation to tubicoly, while the male is a mobile (ambulatory) mating form.

Family Typhlotanaidae Sieg, 1984

Antiplotanais gen. nov.

Diagnosis. Typhlotanaid with large, acuminate apophyses on coxae of pereopods 1–3, each bearing a seta; chela fingers less than half length of cheliped propodus; cheliped carpus with sparse dorsal setae and rounded proximodorsal apophysis; carpus of pereopods 4–6 with ventral ring of setules but no evident spines; antennule of 3 articles, antenna of six articles; mandibular molar process distally with robust tubercles but no setae; maxillule with nine distal spines; uropod rami one-articled.

Type species: *Antiplotanais coochimudlo*, by original designation. Other included species: *Typhlotanais lutze* Bamber, 2005.

Etymology. A hybrid of '*Antip-*' from Antipodean, species having been found only in Australia to date, and '*Typhlotanais*', the genus (*sensu lato*) to which the new genus appears closest.

Remarks. The cumbersome genus *Typhlotanais* Sars, 1882 *sensu lato* contained perhaps seventy described species, of global distribution and occurring in all depths from the littoral to over 6000 m; numerous further taxa are presently being resolved from, for example, the northeast Atlantic (G. J. Bird, pers. comm.). Recently, Błażewicz-Paszkowycz (2004, 2005), while redefining *Peraeospinosus* Sieg, 1986 (comprising species originally attributed to *Typhlotanais* as well as new taxa), pointed out the presence of a number of 'morpho-groups' within *Typhlotanais sensu lato* which warrant distinction as separate genera; subsequently, Błażewicz-Paszkowycz (2007) valuably rationalised 66 species of the Typhlotanaidae into nine genera and a further seven morphogroups.

Both the species newly described below and the similar *Typhlotanais lutze* Bamber, 2005, also from Australia (Western Australia), show consistent features which in combination are distinct from other described taxa within *Typhlotanais*, notably the short chela fingers, the large coxal apophyses on pereopods 1–3 and the cuticular ornamentation of the posterior pereopods. These features are considered sufficient to warrant the separation of these two species into a new genus. The distinctive coxal spur on the anterior pereopods accords with the *greenwichensis*-group of Błażewicz-Paszkowycz (2007), although the body, legs and uropods are more compact than those of *Typhlotanais greenwichensis* and *T. messinensis*; the chela fingers of *T. greenwichensis* are not less-than-half of the length of the chela,

while the uropod rami of *T. messinensis* are both two-segmented. Nevertheless, should the coxal spur be regarded as the defining character, then these taxa may also eventually be included in *Antiplotanais* gen. nov.

Antiplotanais coochiemudlo sp. nov.
(Figs 18, 19)

Material Examined. HOLOTYPE: QM-W28092, ♀, muddy medium sand with shell breccia and holo-thurians, N. of Moreton I., Moreton Bay, 26°56.38'S, 153°23.73'E, 41.3 m, 35‰, 28.8°C, van Veen grab, 16.02.2005, RNB. PARATYPES: QM-W28093, 2 ♀, 2 ♀♀, dissected, data as for holotype. QM-W28094, ♀, coarse sand and shell with *Branchiostoma*, Moreton Bay, 27°27.0'S, 153°18.8'E, 8.4–9.9 m, 10.02.2005, spanner-crab dredge, RNB. NHM 2006. 1540–1541, 2 ♀, sand, north of Banana Bank, Moreton Bay, 27°32.02'S, 153°20.67'E, 4.9m, 11.02.2005, van Veen grab, RBN. QM-W28095, ♀, sandy mud with seagrass, Banana Bank, Moreton Bay, 27°32.46'S, 153°20.74'E, 3.1 m, 17.02.2005, van Veen grab, RNB. OTHER MATERIAL. QM-W28440, ♀, MBWS Stn. 3; QM-W28441, 2 ♀♀, MBWS Stn. 5; QM-W28442, ♀, MBWS Stn. 10; QM-W28443, 4 ♀♀, MBWS Stn. 13, all van Veen grab, PJFD.

Description. Body (Fig. 18A) compact, small (holotype 1.73 mm long, 4.8 times as long as wide). Cephalothorax subrectangular, 1.2 times as long as wide, longer than pereonites 1, 2 and 3 together, naked, eyes absent. Six free pereonites; pereonites 1 and 2 shortest, pereonites 3 and 6 subequal, 1.2 times as long as pereonite 1, pereonites 4 and 5 subequal, 1.5 times as long as pereonite 1 (all pereonites respectively 2.8, 2.8, 2.4, 1.9, 2 and 2.6 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite 6 times as wide as long. Pleotelson semicircular, as long as last three pleonites, with one midlateral and one postero-lateral seta on each side and two distal setae.

Antennule (Fig. 18B) of three articles, proximal article three times as long as wide, 1.6 times as long as distal two articles together; second article as long as wide, 0.3 times as long as third article; third article tapering, with eight distal setae, one of these twice as wide as the others.

Antenna (Fig. 18C) of six articles, proximal three articles compact, subequal, second article with ventrodistal seta; fourth article longest, 3.8 times as long as wide, with one distal seta; fifth article half as long as fourth, with one long and

one short distal seta; sixth article smallest with four distal setae.

Labrum (Fig. 18E) rounded, setose. Left mandible (Fig. 18G) with wide, crenulate lacinia mobilis, right mandible (Fig. 18F) without lacinia mobilis; pars molaris of both mandibles with strong, rounded tooth-like protrusions. Labium simple, finely setose, without palp. Maxillule (Fig. 18D) with nine distal spines, palp with two distal setae; maxilla (Fig. 18D) simple, kidney-shaped. Maxilliped palp (Fig. 18H) first article naked, second article with three inner setae, third and fourth articles with filtering rows of four and six setae respectively; basis with single, long seta not reaching distal margin of endites; endites distally with single outer seta and oval membranous structure.

Cheliped (Fig. 19A) with rounded basis 1.8 times as long as wide, merus subtriangular with single ventral seta; carpus with rounded dorso-proximal extension, elongate, 2.6 times as long as wide, with three midventral setae and sparse, short setae on dorsal margin; propodus slender 0.85 times as long as carpus, fixed finger with two ventral and one inner setae, three setae on cutting edge; dactylus with fine dorsal seta; chela fingers 0.4 times as long as whole propodus.

Pereopod 1 (Fig. 19B) longer than others, coxal apophysis large, pointed, with seta; basis slender, 2.8 times as long as wide; ischium compact; merus 0.75 times as long as carpus, with single ventrodistal seta; carpus with two distal setae; propodus 1.4 times as long as carpus, with three distal setae; dactylus with distinct, longer, slender claw, both together 0.8 times as long as propodus. Pereopod 2 (Fig. 19C), coxa and basis similar to pereopod 1; ischium with single seta; merus and carpus subequal, merus with single ventral seta, carpus with paired ventrodistal setae and rows of fine setules; propodus 1.4 times as long as carpus, with paired ventro-distal stout spines, one laterodistal and two dorsodistal setae; dactylus with slender, subequal claw 0.6 times as long as propodus. Pereopod 3 compact (Fig. 19D), similar to pereopod 2.

Pereopod 4 (Fig. 19E) basis longer, 2.4 times as long as wide with ventrodistal plumose sensory seta; otherwise as pereopod 5. Pereopod 5 (Fig. 19F, G) coxa simple; basis stout, 1.6 times as long as wide; ischium with single ventrodistal
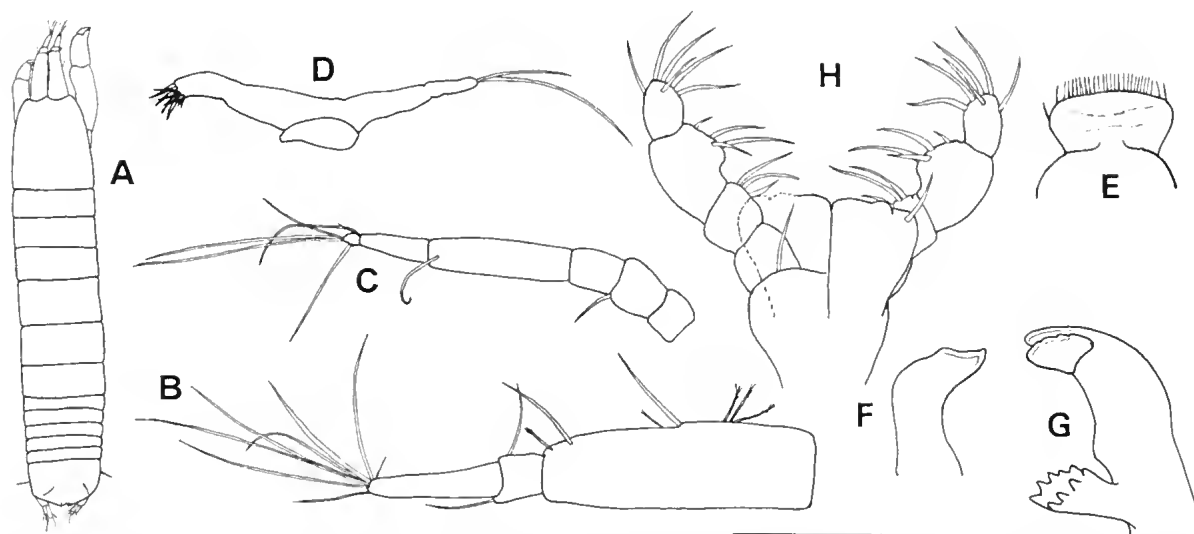
FIG. 18. *Antiplotanais coochimudlo* sp. nov. , **A**, holotype female, dorsal; **B**, antennule; **C**, antenna; **D**, maxillule and maxilla; **E**, labrum; **F**, right mandible; **G**, left mandible; **H**, maxilliped. Scale bar = 1 mm for A; 0.15 mm for B–D; 0.1 mm for E–H.

seta; merus with paired ventrodistal stout spines and ventral rows of fine setules; carpus as long as merus, with dorsodistal seta and ventral prickly tubercles *sensu* Błażewicz-Paszkowycz (2007); propodus longer than carpus, with paired ventrodistal stout spines, ventral rows of fine setules, and one short and one long dorsodistal setae; dactylus and unguis appeasring to be fused into claw, curved. Pereopod 6 (Fig. 19H) as pereopod 5, but propodus with three distal setae.

Pleopods (Fig. 19I) all alike, with naked basis; endopod with inner distal seta, exopod without setae on inner margin, outer margins with respectively 8 and 12 plumose setae, most proximal seta separated from the remainder.

Uropod (Fig. 19J) biramous, both exopod and endopod of one segment; exopod 0.8 times as long as endopod, with two distal and one subdistal setae; endopod with four distal setae.

Male unknown.

Etymology. Coochiemudlo is the Goenpul Aboriginal name for an island south of Banana Bank, Moreton Bay.

Remarks. With its combination of a short chela and pronounced, seta-bearing apophyses on the anterior coxae, the present species is closest to *Antiplotanais lutze* (Bamber 2005) comb. nov. Close examination of paratypic material of *A. lutze* has discerned the presence of fields of fine

setules and prickly tubercles on the ventral margins of merus, carpus and propodus of pereopods 4–6 in that species also, as described above for *A. coochimudlo* sp. nov. Equally, both species show a similar paucity of the pereopod setation/spination, and otherwise consistent morphology of mouthparts, pleopods, uropods, etc.

Antiplotanais coochimudlo can be distinguished from *A. lutze* (from southwestern Australia) in having much more slender antennule articles, more compact bases to the anterior pereopods, one longer and one shorter setae dorsodistally on the propodus of pereopods 4–6 (two longer setae in *A. lutze*), three setae on the uropod exopod (two setae in *A. lutze*), and in the proportions of the cheliped articles (e.g. carpus longer than propodus, and merus extending to midpoint of ventral margin of carpus in *A. coochimudlo*, carpus and propodus of equal length, and merus hardly reaching one-third the length along the ventral margin of the carpus in *A. lutze*). Both are distinguished from the species of the *greenwichensis*-group as described above under the generic Remarks.

Family Paratanaidae Lang, 1949
Subfamily Bathytanaidinae
Larsen & Heard, 2001

Bathytanais Beddard, 1886
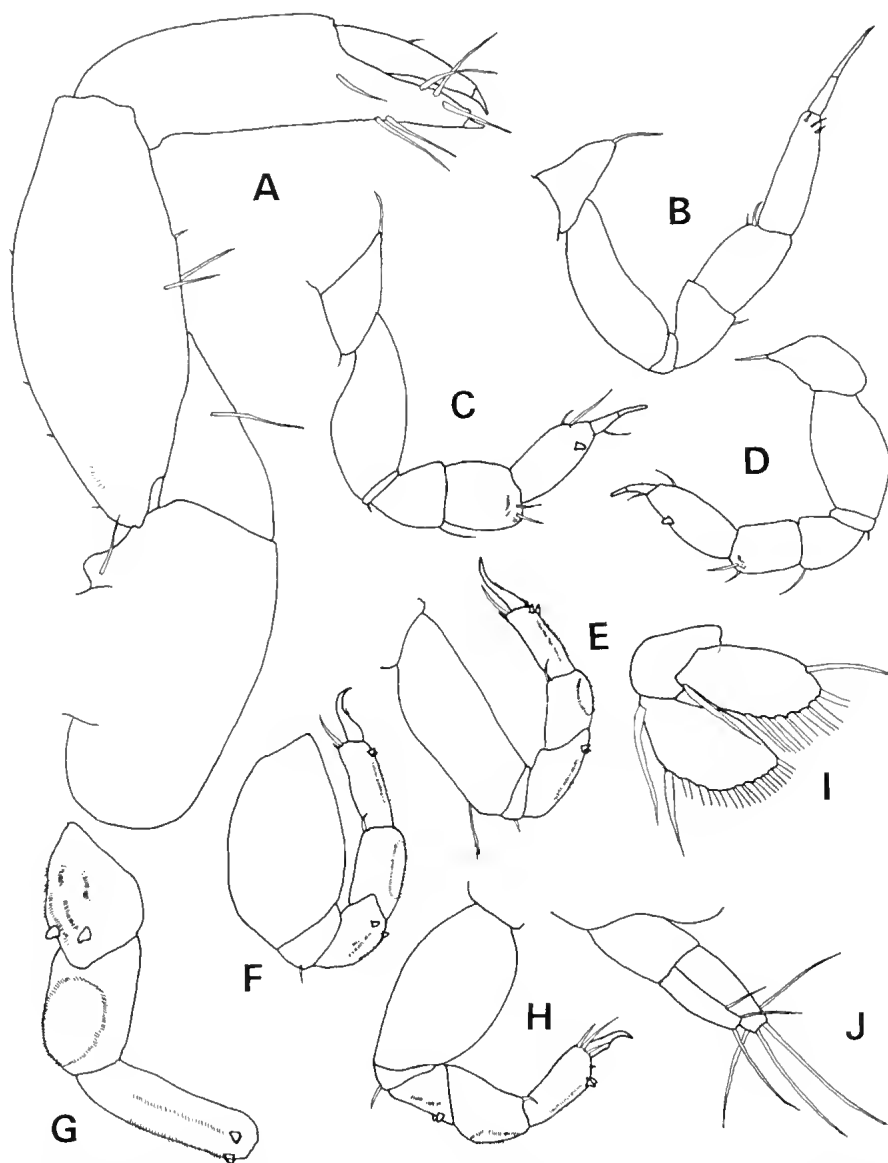
FIG. 19. *Antiplotanais coochimudlo* sp. nov., **A**, cheliped; **B–F**, pereopods 1–5 respectively; **G**, merus, carpus and propodus of pereopod 5, ventrolateral detail; **H**, pereopod 6; **I**, pleopod; **J**, uropod. Scale bar = 0.1 mm for A–F, H–J; 0.05 mm for G.

Bathytanais bathybrotes (Beddard, 1886)

Paratanais bathybrotes Beddard, 1886a: 119.
Bathytanais bathybrotes — Beddard, 1886b: 133–134, plate 17; Lang, 1972: 221–229, figs 1–5; Larsen & Wilson, 1998: 347–348, fig. 9 (literature).

Material Examined. QM-W28096, brooding ♀, 2 ♀♀ without oostegites, 2 juvs, brooding ♀, dissected, clean medium sand with some shell, dense holothurians, off South Passage East of Moreton I., 27°

17.54'S, 153°28.26'E, 29 m, 35‰, 28.1°C, 19.02.2005, van Veen grab, RNB. QM-W28097, 3 ♀♀ without oostegites, muddy medium sand with shell breccia and holothurians, N. of Moreton I., Moreton Bay, 26°56.38'S, 153°23.73'E, 41.3 m, 35‰, 28.8°C, 16.02.2005, van Veen grab, RNB. NHM 2006.1542–1543, 2 ♀♀ without oostegites, clean medium sand with shell breccia, N. of Moreton I., Moreton Bay, 26°56.89'S, 153°24.19'E, 23.6 m, 35‰, 28.3°C, 16.02.2005, van Veen grab, RNB. NHM 2006.1544, ♀ without ooste-

gites, slightly muddy medium sand with holothurians, NW of Flat Rock, East of South Passage, 27°22.95'S, 153°30.79'E, 26.6 m, 35‰, 28°C, 19.02.2005, van Veen grab, RNB. QM-W28098, ♀, 1 juv, slightly muddy medium sand with holothurians, NW of Flat Rock, East of South Passage, 27°22.10'S, 153°31.91'E, 35.5 m, 35‰, 27.9°C, 19.02.2005, van Veen grab, RNB. 3 ♀♀, NHM 2006.1545–1549, 2 juvs, coarse sand with shell and holothurians, East of Moreton I., 27°13.07'S, 153°28.29'E, 35.6 m, 35‰, 22.02.2005, van Veen grab, RNB. QM-W28099, ♀, medium sand with shell, west of Moreton I., 27°04.10'S, 153°16.95'E, 8.5 m, 35‰, 23.02.2005, van Veen grab, RNB.

Remarks. *Bathytanais bathybrotes* was first described by Beddard (1886a) on the basis of a single female reportedly taken from 3,752 m from the North Pacific (north-east of Midway I.). In his more detailed *Challenger Report* (Beddard 1886b) he reported a further 14 individuals from Port Jackson, New South Wales, Australia at 6–18 m depth. Subsequently, Lang (1972) recorded a specimen from 50 m off Grafton, New South Wales (*Galathea* Stn 544), and gave a comprehensive redescription. The present material accords with the surviving Port Jackson specimens of Beddard (1886b) (NHM.1967:11:12.1–9) and with the description of Lang (1972; but note Larsen & Wilson's (1972) comments on the cheliped basis) other than the articulation of the uropod rami, with the exopod here showing no apparent articulation, and the endopod showing marked fusion of two articles (see also Larsen & Wilson 1998). It also accords with a southeastern Australian distribution, and adds further doubt to the location (and unlikely depth) of Beddard's holotype (now lost).

While largely characterised by the conformation of the lobes on the antennal peduncle articles 2 and 3, a notable feature of this species is the ventral 'flange' on the basal peduncle article of the antennule (Beddard, 1886b, Pl. 17, Fig. 12; Lang, 1972, Fig. 1d), present even in juveniles. Unlike the comments of Larsen & Wilson (1998) the present material, as that of Lang (loc. cit.) has seven distal spines on the maxillule endite.

Other than the holotype of doubtful provenance, all specimens have been found on clean sand at depths between 6–50 m; the twenty specimens in the present material were all taken outside Moreton Bay, off the major sand banks of Moreton and North Stradbroke Islands.

Bathytanais culteriformis Larsen & Heard, 2001

Bathytanais culteriformis Larsen & Heard, 2001: 3–7, figs 1, 2.

Material Examined. QM-W28100, ♀ without oostegites, muddy sand with spatangoids, Moreton Bay, 27°20.91'S, 153°19.96'E, 16.6 m, 33‰, 29.1°C, 10.02.2005, van Veen grab, RNB. QM-W28101, ♀ without oostegites sand, north of Banana Bank, Moreton Bay, 27°32.02'S, 153°20.67'E, 4.9 m, 11.02.2005, van Veen grab, RNB. QM-W28444, subadult ♀, dissected, coarse sand and shell with *Branchiostoma*, Moreton Bay, 27°27.0'S, 153°18.8'E, 8.4–9.9 m, 10.02.2005, spanner-crab dredge, RNB, ♀, MBWS Stn. 4; QM-W28445, 2 ♀♀, MBWS Stn. 10; QM-W28446, ♀, MBWS Stn. 13; QM-W28447, ♀, MBWS Stn. 15; all van Veen grab, PJFD. QM-W12582, 22 ♀♀, one in a mucus tube, Middle Banks, northern Moreton Bay, 17.09.1983/13.01.1984, P. Saenger & S. Cook (there are two dates on the label, in material containing a number of species).

Remarks. These specimens, all collected from sandy substrata within Moreton Bay at depths from 4.9–16.6 m, are almost identical to the figures and type-descriptions of *B. culteriformis* (see Larsen & Heard 2001), although that material was collected from north-west Australian waters (again on sand, at 38–88 m depth). In particular, the antennal morphology is typical for that species. The chela dactylus has two fusiform setae on the cutting edge, and there is a distinct row of eight denticulate setae along the propodal distal margin at the insertion of the dactylus (about three indicated by Larsen & Heard 2001, for their dissected paratype).

Bathytanais juergeni Larsen & Wilson, 1998

Bathytanais juergeni Larsen & Wilson, 1998: 348–357, figs 1–9.

Material Examined. QM-W28102, ♀ without oostegites in *Phoronis* tube mat, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005, A-NL. QM-W28103, 1 manca sponge and bryozoan epifauna, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005, A-NL. 1 manca, dissected on *Sertularella diaphana* with ectozoic *Hebella* sp., Amity Point, 27°23.9'S, 153°26.2'E, 5–10 m depth (dive), 14.02.2005, A-NL.

Remarks. *Bathytanais juergeni* was originally described from Bute Bay, New South Wales at depths of 45–50 m, living in tubes on a sandy substratum. The present material was collected in epifaunal habitats, at 5–10 m depth, all off the northern coast of North Stradbroke Island. The dorsal spine on article 3 of the antennal peduncle

shows an articulation with the article, and the antennal peduncle articles are somewhat more slender (length of article 1 2.9 times the width in the adult female, twice as long in the type-description). Otherwise, the Moreton Bay material is consistent with the figures and descriptions of the types.

While the presence of three sympatric species of *Bathytanais* in the Moreton Bay area was at first surprising, they in fact occur in separate habitats (at least here), with *B. culteriformis* in the sheltered sands of Moreton bay, *B. bathybrotes* in sands in the open Pacific waters offshore of the islands to the east of the Bay, and *B. juergeni* in epifaunal habitats. As well as by habitat, they are all distinguishable by the morphology of the antenna (other morphology being generally conservative in this genus). A key to the species of *Bathytanais* was given by Larsen & Heard (2001), since when the only new species described has been *B. greebo* Bamber, 2005, taken in medium to coarse sands at 29–33 m depth off Esperance, Western Australia; this last is distinct as being the only species without a dorsodistal apophysis on the third peduncle article of the antenna, although a ventrodistal apophysis is present (Bamber 2005). Disregarding the suspect type-locality of *B. bathybrotes* (see above), all species are from Australian waters except for *B. bipennifer* Bird & Bamber, 2000 (*q.v.*), recorded from Hong Kong.

Subfamily **Teleotanaidinae nom. nov**.

Teleotanais Lang, 1956

Revised diagnosis. Female small, elongate paratanaid with mottled dorsal pigmentation, dorsoventrally flattened, cephalon with slight rostrum, eyelobes and pigmented eyes. Six free pereonites, five free pleonites, the first four bearing articulated plumose midlateral setae. Antennule of four articles, antenna of six articles without dorsodistal spine on third article, distal setae simple. Maxillule with palp bearing one or two distal setae; maxilliped endite not expanded, distally with single seta and two or three fine pointed spines. Anterior pereopods setose, with slender dactylus plus unguis; posterior pereopods withy distal spines on merus, carpus and propodus; dactylus plus unguis slender, not fused into a claw; pleopods biramous, basis

with single dorsal plumose seta; uropods short, biramous; exopod of two segments, endopod of one or two segments.

Type Species: *Teleotanais gerlachi* Lang, 1956. Other included species: *Teleotanais warragamba* sp. nov.; *Teleotanais 'gerlachei'* Sieg & Heard, 1983 (Nigerian material)

Remarks. *Teleotanais* has the immediate overall appearance of a paratanaid, and the pleonites bear the articulated midlateral plumose setae characteristic of that family, although not recognised as such by Lang (1956), while Sieg (1976) and Sieg & Heard (1983) make no mention of pleonite setae. However, the maxilliped endites are not expanded, as they are in all other paratanaid genera, and the sharp distal spines are unusual, other paratanaids having flat, rounded distal endite spines. Further, the ungues of the posterior pereopods are less reduced than in any other paratanaid genus. Although Lang (*loc. cit.*) attributed his new genus to the Paratanaidae, Sieg & Heard (1983) attributed the genus to the Nototanaidae (and then went on to compare it only with *Paratanais*!) on the basis of its having fused maxilliped bases; owing to the conformation of the maxilliped endites and the lack of knowledge of the articulated plumose pleonite setae subsequent researchers have put the genus in the Nototanaidae (e.g. Guţu & Sieg 1999; Larsen & Wilson 2002; Anderson *et al.* 2007). From the additional information from the present, second species of the genus, it is clearly a member of the Paratanaidae.

Teleotanais warragamba **sp. nov**.
(Figs 20, 21)

Material Examined. HOLOTYPE: QM-W28104, brooding ♀, 14 ♀♀ (11 brooding), 4 mancae. PARATYPES: QM-W28105, 3 brooding ♀♀, NHM 2006.1550–1552, amongst algae on low-tide wreck, Bradbury Beach, Dunwich, North Stradbroke I., 27°29'S, 153°24'E, littoral, 21.02.2005, D. Jones.

Description. Female body (Fig. 20A) slender, small, holotype 2.2 mm long, 7 times as long as wide. Cephalothorax subrectangular, 1.3 times as long as wide, as long as pereonites 1, 2 and 3 together, tapering to anterior with slight rostrum, eyelobes with eyes present and black. Six free pereonites; pereonite 1 shortest, pereonite 2 slightly longer, pereonites 3, 4 and 6 subequal, pereonite 5 longest and 2.7 times as long as

pereonite 1 (all pereonites respectively 3.0, 2.4, 1.8, 1.5, 1.1 and 1.6 times as wide as long). Pleon of five free pleonites progressively shorter posteriorly, each bearing pleopods; each pleonite about 4 times as wide as long, with single articulating, plumose midlateral setae. Pleotelson semicircular, as long as last two pleonites together, 1.5 times as wide as long, with on each side single lateral setae anterior of uropod insertion, three posterior of uropod insertion and two mid-distal setae. Black mottled pigmentation (reminiscent of that of a *Tanais*) present over the whole dorsum, also on chelae and slight pigment spots on antennules.

Antennule (Fig. 20B) of four tapering articles, proximal article 2.15 times as long as wide, 0.9 times as long as distal three articles together, with long outer distal seta; second article just longer than wide, distal outer seta as long as article; third article two-thirds length of second; fourth article just longer than second, with three distal setae, four subdistal setae and two subdistal aesthetascs implying fusion of a small fifth article.

Antenna (Fig. 20C) of six articles, proximal article compact, naked; second article as long as wide, naked; third article longest, three times as long as first and 2.2 times as long as wide, with dorsal row of three strong setae; fourth article 0.75 times as long as third with long ventrodistal seta; fifth article 0.8 times as long as fourth; sixth article minute.

Labrum (Fig. 20D) rounded, setose. Left mandible (Fig. 20F) with crenulate lacinia mobilis not wider than crenulate pars incisiva, pars molaris stout with strong rugosity; right mandible (Fig. 20E) similar but without lacinia mobilis. Labium (Fig. 20G) wide, bilobed, distally finely setose, without palp. Maxillule (Fig. 20H) with nine distal spines; palp distinct, with single distal seta; maxillule rounded, simple. Maxilliped (Fig. 20I) palp first article naked, second article with one outer and three inner simple setae; third and fourth articles with filtering rows of six and eight setae respectively, third article with two further inner distal setae, fourth article with outer seta; basis with single long seta extending to third palp article; endites (Fig. 20J) narrower than bases, distally with single seta and two short, sharp spines. Epignath not seen.

Cheliped (Fig. 21A) with rounded, compact basis 1.25 times as long as wide; merus subtriangular with two ventral setae; carpus 1.74 times as long as wide, with two ventrodistal setae; propodus robust, fixed finger with three ventral and three inner setae, cutting edge expanded into blade along distal two-thirds; setal row at base of dactylus of four setae; dactylus with proximal seta, small spine proximally on cutting edge.

Pereopod 1 (Fig. 21B) longer than other pereopods, coxa with seta; basis slender, 3.9 times as long as wide; ischium with one seta; merus 1.4 times as long as carpus, with single ventrodistal seta; carpus with three distal setae; propodus just longer than carpus, with five distal setae; dactylus slender, extending into subequal slender unguis, the two together 1.25 times as long as propodus. Pereopods 2 and 3 (Fig. 21C) similar to each other, more compact than pereopod 1; basis 3.2 times as long as wide; ischium with one seta; merus just shorter than carpus, merus with two ventrodistal spine, carpus with dorsodistal and ventrodistal seta; dactylus and subequal unguis together 1.2 times as long as propodus.

Pereopods 4 and 5 (Fig. 21D) similar to each other, basis stouter, 2.34 times as long as wide; ischium with one seta; merus longer than carpus, with two ventrodistal spines, carpus with outer, ventral and inner distal spines; propodus as long as merus, with two ventrodistal spines, three distal setae as long as dactylus; dactylus and unguis partially fused into a claw, curved, shorter than propodus. Pereopod 6 (Fig. 21E) as pereopod 4, but distal propodal spines more slender, propodus with four distal setae.

Pleopods (Fig. 20K) all alike, with single inner plumose seta on basis; endopod with two inner setae.

Uropod (Fig. 21F) biramous, basis naked; exopod of two subequal segments, outer distal seta longer than inner distal seta; endopod of one segments, 1.25 times as long as exopod.

Male unknown.

Etymology. *Warragamba* is the name of a sand bank in Moreton Bay.

Remarks. *Teleotanais warragamba* sp. nov. differs from the only previously described species, *T. gerlachei*, in its more compact third antennule
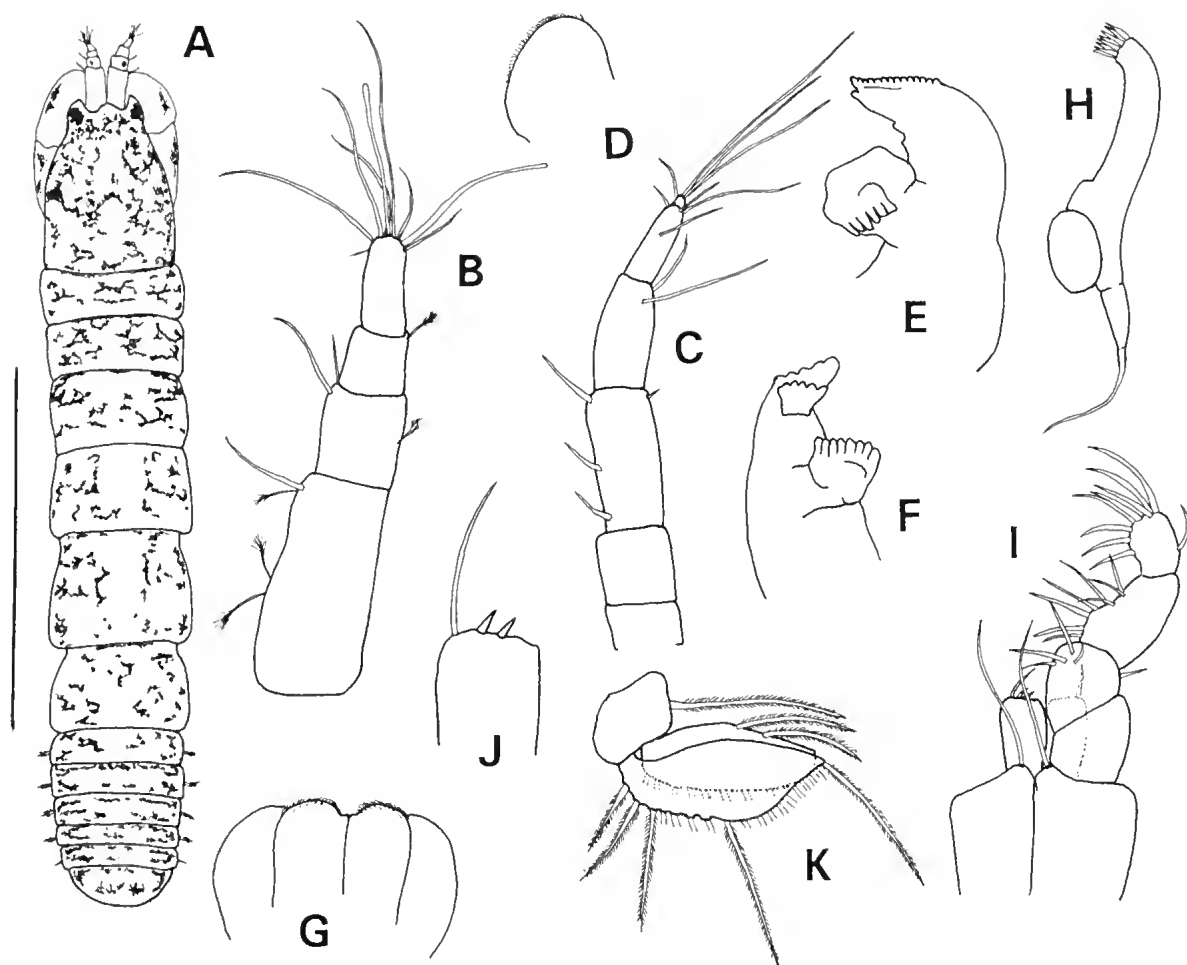
FIG. 20. *Teleotanais warragamba* gen. et sp. nov., **A**, holotype, dorsal; **B**, antennule; **C**, antenna; **D**, labrum, lateral; **E**, right mandible; **F**, left mandible; **G**, labium; **H**, maxillule and maxilla; **I**, maxilliped; **J**, detail of maxilliped endite; **K**, pleopod. Scale bar = 1 mm for A; 0.2 mm for B–I, K; 0.1 mm for J.

article, in having only two (rather than three) sharp distal spines on each maxilliped endite, a comparatively longer dactylus and unguis on pereopod 1, and only one segment in the uropod endopod (two in *T. gerlachei*).

Sieg & Heard (1983) include in their analysis of *T. gerlachei* from Florida some 200 specimens from Port Hartcourt, Nigeria, but their redescription and stylised figures (copied from Sieg 1976) are based on specimens from El Salvador. It seems inconceivable that the Nigerian material is conspecific with Lang's South American-Caribbean species, unless its presence in Africa is a result of anthropogenic transport, e.g. in fouling on the hull of a ship. A more

critical examination of that material is warranted in the light of the discovery of *T. warragamba*. Similarly, while the records of Sieg (1976) from Panama were mis-identifications (Sieg & Heard 1983), his material from Pacific El Salvador attributed to *T. gerlachei* needs critical re-examination.

The midlateral pleonite setae of *Teleotanais* are diagnostic of the Paratanaidae, while none of the 'non-paratanaid' features of narrow maxilliped endites with small, sharp distal spines, the slender posterior ungues are diagnostic of any other genus. As these features appear to be plesiomorphic in comparison to their counterparts in described paratanaids, *Teleotanais*
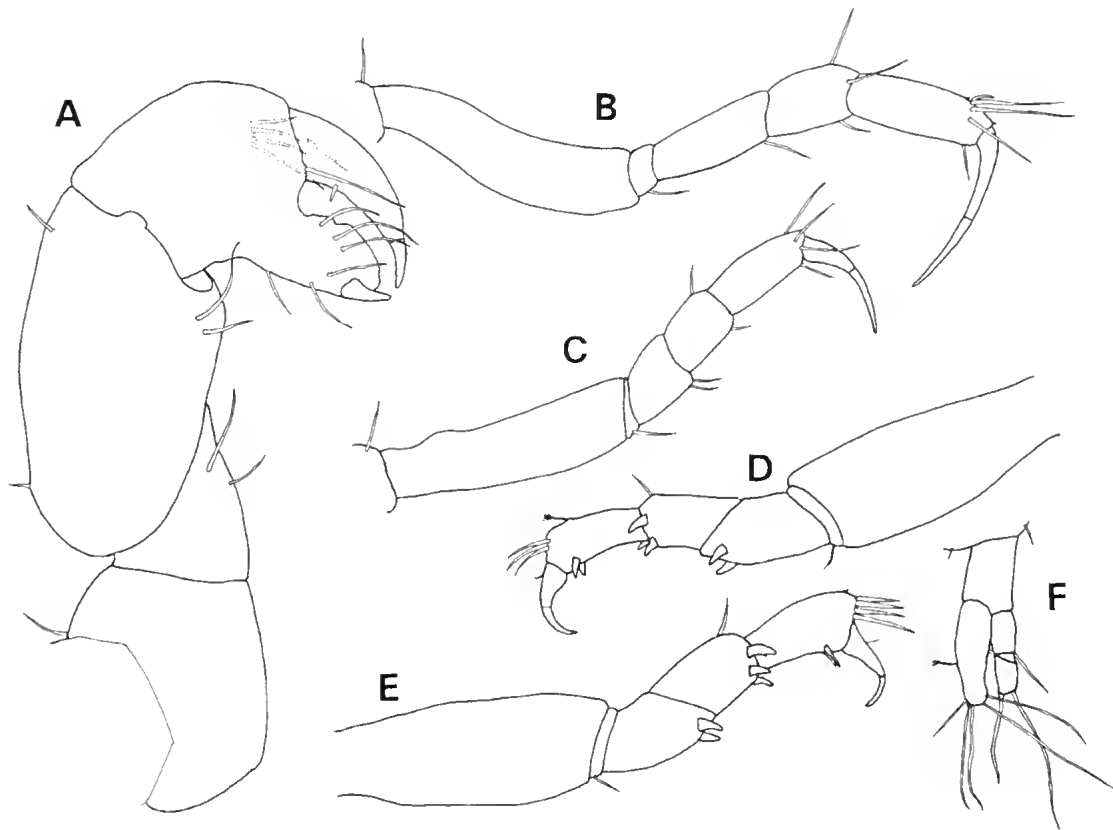
FIG. 21. *Teleotanais warragamba* gen. et sp. nov., **A**. Cheliped; **B**, pereopod 1; **C**, pereopod 3; **D**, pereopod 5; **E**, pereopod 6; **F**, uropod. Scale bar = 0.1 mm.

appears to be a primitive member of the family, with less specialised maxilliped endites, anterior pereopod setation and posterior ungues. In the context of the subfamily divisions of Larsen & Heard (2001), *Teleotanais* is herein placed in its own subfamily, the Teleotanaidinae, with the characters of the genus. Equally, these are the only littoral species of the family (*T. gerlachei* was recorded from the low littoral and near mangroves at a number of sites in Brazil, and from reduced salinity mangrove habitat in El Salvador and Florida), which may account for the unusual (for a paratanaid) pigmentation; Lang does not describe the colouration of the types of *T. gerlachei*, but Sieg & Heard (1983) figure the colouration of their material, although without specifying whether it is from Florida or from Nigeria; no other paratanaid is described as bearing mottled dorsal pigmentation.

Subfamily Paratanaidinae Lang, 1949

Paratanais wanga sp. nov.
(Figs 22–24)

Material Examined. HOLOTYPE: QM-W28106, ♀, QM-W28107, ♂ allotype, ♀, 2 juvs. PARATYPES: QM-W28108, ♀, dissected, in filamentous red algae, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. NHM 222006.1553, ♀ in *Phoronis* tube mat, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28109, 2 ♀♀ amongst barnacle-sponge epifaunal on tyres, off Amity Point, North Stradbroke I., 27°23.9'S, 153°26.2'E, 8–10 m, 35‰, 14.02.2005. NHM 2006.1554–1559, 5 ♀♀, 1 manca, (amongst sponges (*Niphatis*), Amity Point, 27124.9'S, 153126.22'E, 4–9 m, 15.02.2005. QM-W28110, subadult ♀? on the bryozoan *Orthoscuticella ventricosa* agg, Henderson's Pinnacles, east side of Moreton I., 27°07.901'S, 153°28.712'E, 22–26 m, 22.02.2005, all A-NL.

Description of female. Body (Fig. 22A) slender, holotype 3.4 mm long, 6.4 times as long as wide. Cephalothorax tapering towards the rostrum, 1.1 times as long as wide, 1.3 times as long as pereonites 1 and 2 together, with slight rostrum,

eyelobes and eyes present and black, single setae at posterior of eyelobes and midlaterally. Six free pereonites; pereonite 1 shortest, pereonites 2 and 3 subequal and 1.5 times as long as pereonite 1, pereonites 4–6 subequal and 1.3 times as long as pereonite 2 (all pereonites respectively 3.1, 2.1, 2.1, 1.7, 1.65 and 1.7 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 6.7 times as wide as long, pleonites 1–4 with plumose mid-lateral seta on each side, pleonite 5 with simple midlateral seta. Pleotelson semicircular, just longer than last two pleonites together, 2.3 times as wide as long, with single lateral setae on each side above uropod attachment and two distal setae.

Antennule (Fig. 22C) of four articles, proximal article 1.6 times as long as wide, with single median blunt seta and adjacent plumose seta; second article one third as long as first, longer distal outer seta blunt; third article 0.75 times as long as second, with blunt distal seta; fourth article longer than second and third together, with four distal setae and one aesthetasc.

Antenna (Fig. 22D) of six articles, proximal article compact, naked; second article 1.4 times as long as wide, with single dorsodistal spine and setulose dorsal margin; third article 0.6 times as long as wide, with stout dorsodistal spine; fourth article twice as long as third, with longer distal seta blunt and exceeding antenna tip; fifth article half as long as fourth with blunt distal seta more than twice length of article; sixth article minute with five distal setae.

Labrum rounded, setose, typical of genus. Left mandible (Fig. 22E) with crenulate lacinia mobilis, little crenulation on pars incisiva, pars molaris robust with marginal rugosity; right mandible (Fig. 22F) similar but without lacinia mobilis, pars molaris simpler. Labium simple with rows of fine setules, without palp. Maxillule (Fig. 22J) with eight distal spines of which inner pair are shortest, setose outer margin; palp distinct, with two distal setae. Maxilliped (Fig. 22I) palp first article naked, second article with one simple outer and three finely-denticulate inner setae; third article with five finely-denticulate inner setae; fourth article with three inner finely-denticulate inner setae, distal and outer setae simple; basis with one simple seta extending past tip of first palp article;

endites (Fig. 22H) with serrated and setulose laterodistal margins, each with two linguiform distal spines but no distal seta. Epignath (Fig. 22G) elongate with setose distal margins.

Cheliped (Fig. 23A) with rounded, compact basis 1.25 times as long as wide; merus subtriangular with single blunt ventral seta; carpus 1.5 times as long as wide, with two blunt ventrodistal setae; propodus typical for the genus, fixed finger with two ventral and three inner blunt setae, cutting edge slightly crenulate, setal row at base of dactylus of three setae; dactylus with proximal seta and two leaf-like spines on proximal half of cutting edge.

Pereopod 1 (Fig. 23B) longer than other pereopods, coxa naked; basis slender, 5.5 times as long as wide with short, blunt dorsal seta in proximal half; ischium compact with one blunt seta; merus 1.3 times as long as carpus, naked; carpus with two distal setae; propodus 1.5 times as long as carpus, with three distal setae; dactylus slender, extending into longer slender unguis, the two together 1.3 times as long as propodus; single distal seta on dactylus. Pereopods 2 and 3 (Fig. 23C) similar to each other, more compact than pereopod 1; basis 2.6 times as long as wide; ischium with 2 setae; merus almost as long as carpus and with paired dorsoventral spines; carpus with curved outer and inner distal spines with finely crenulate ventral margins, and paired, shorter ventrodistal spines; propodus 1.7 times as long as carpus, with ventrodistal blunt seta; dactylus and longer unguis slender, together 1.15 times as long as propodus.

Pereopod 4 (Fig. 23D) basis stout, 1.3 times as long as wide with ventral plumose sensory seta; ischium with two setae; merus and carpus subequal, merus with paired ventrodistal spines each with outer setule; carpus with outer, ventral and inner distal spines each with fine outer setule; propodus nearly twice as long as carpus, with distal seta, ventrodistal simple spine and mid-dorsal plumose sensory seta; dactylus and shorter unguis not fused but forming a claw, curved, together half as long as propodus. Pereopod 5 as pereopod 4, but without sensory plumose seta on propodus. Pereopod 6 (Fig. 23E) as pereopod 4, but distal carpal and propodal spines larger, propodus with three pectinate distal setae.
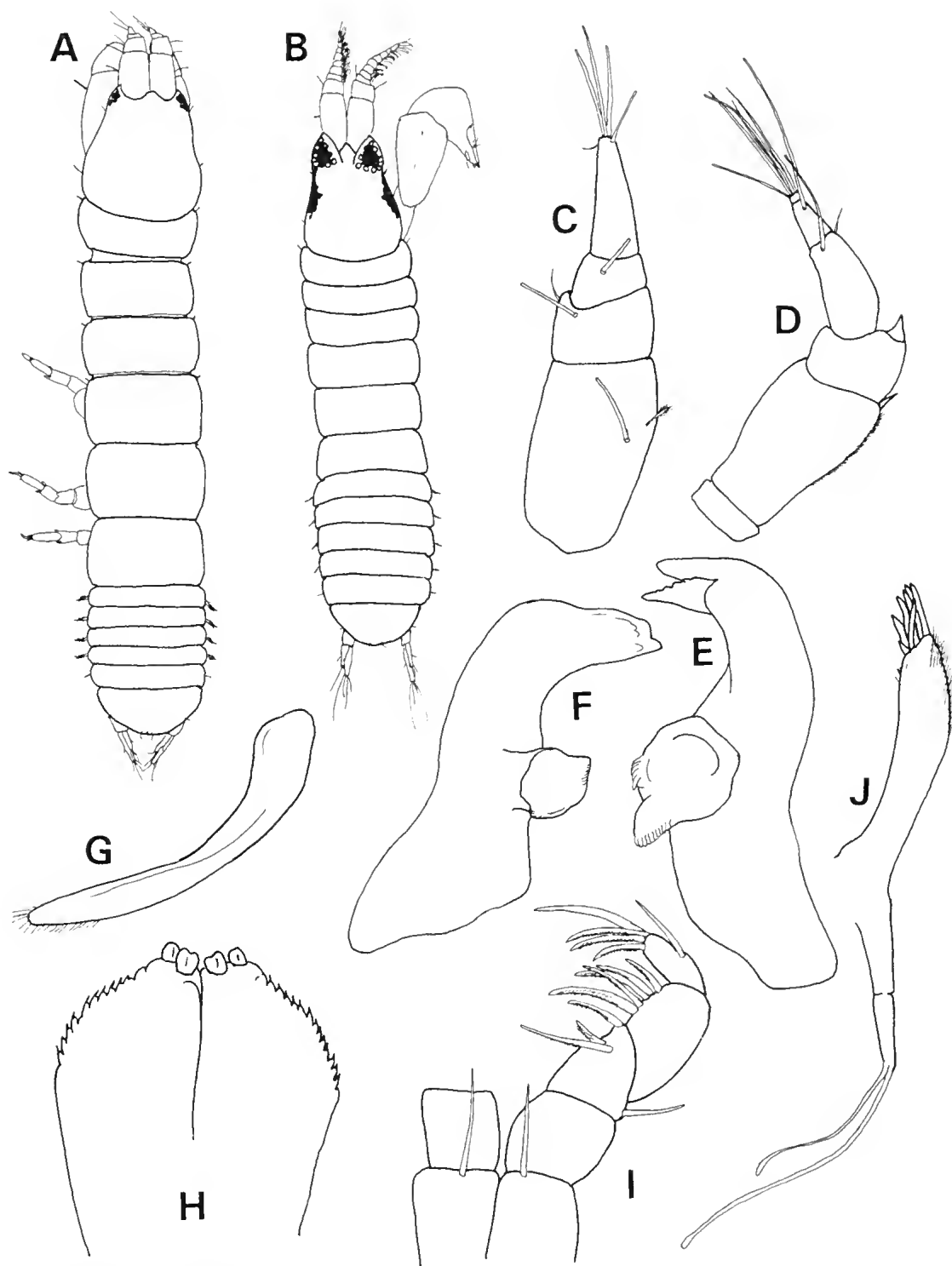
FIG. 22. *Paratanais wanga* sp. nov., **A**, holotype female, dorsal; **B**, allotype male, dorsal; **C–J**, female paratype: **C**, antennule; **D**, antenna; **E**, left mandible; **F**, right mandible; **G**, epignath; **H**, maxilliped endite; **I**, maxilliped; **J**, maxillule. Scale bar = 1 mm for A, B; 0.3 mm for C, D; 0.15 mm for E–J.
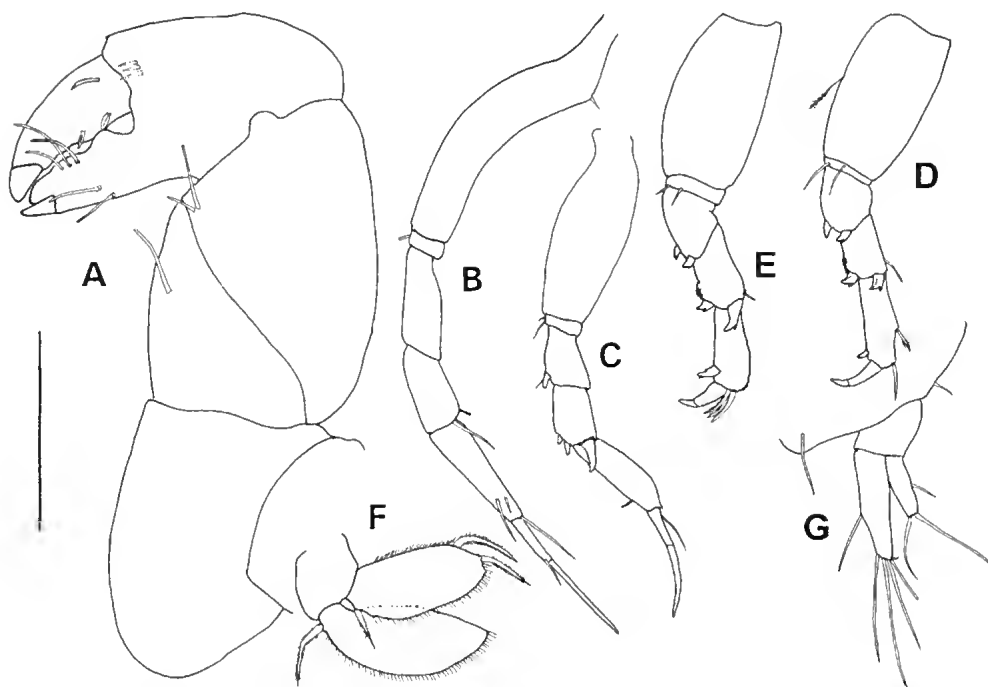
FIG. 23. *Paratanais wanga* sp. nov., **A**, cheliped; **B**, pereopod 1; **C**, pereopod 3; **D**, pereopod 4; **E**, pereopod 6; **F**, pleopod (most setae shown only by their bases); **G**, uropod. Scale bar = 0.3 mm.

Pleopods (Fig. 23F) all alike, typical for the genus, basis naked, endopod with single inner distal plumose seta and 20 outer plumose setae, exopod with 30 outer plumose setae.

Uropod (Fig. 23G) biramous, basis naked; exopod of one segment, 0.6 times as long as endopod, with mid-length outer seta and outer distal seta longer than inner distal seta; endopod of one segment, with mid-length inner seta and four distal setae.

Description of male. Smaller than female (allotype length 2.63 mm), body (Fig. 22B) more compact, cephalon nearly as long as pereonites 1–4 together, with large eyelobes bearing large black eyes, midlateral black pigment patches; pereonites 1–3 subequal (pereonite 1 shortest), pereonites 4–6 subequal (pereonite 5 longest), 1.7 times as long as pereonite 1. Five free pleonites, subequal in length, each 0.9 times as long as pereonite 1, pleotelson twice as long as pleonite 5. Sexual dimorphism as follows.

Antennule (Fig. 24A) elongate, first peduncle article twice as long as wide with single dorsodistal seta; second article one third as long as first with single ventrodistal blunt seta; third article compact, with dorsodistal blunt seta; flagellum of 7 segments, bearing ventrodistal rows of 20, 18, 16, 8, 4, 4 and 1 aesthetascs respectively, distal article also with three shorter, two longer and one blunt setae.

Antenna (Fig. 24B) more slender than that of female, dorsodistal seta rather than spine on article 3, distal setae elongate.

Mouthparts largely atrophied, maxilliped (Fig. 24C) with fewer but much longer and more slender setae.

Cheliped (Fig. 24D) slightly more robust than that of female; carpus 1.13 times as long as wide; propodus distal setal; row of 17 setae; dactylus with slender setae on cutting edge. Pereopods similar to those of female; pereopods 1 (Fig. 24E) 2 and 3 (Fig. 24F) dactylus plus unguis shorter than propodus, pereopods 2–6 with more slender bases, distal spines on carpus more slender than on female, and unguis finely crenulate ventrally; pereopod 6 (Fig. 24G) without ventrodistal spine on propodus.

Pleopods more setose than those of female. Distal setae of uropod rami proportionately longer.

Etymology. Named for Wanga Wallen Bank, a sand-spit just south of Amity Point.

Remarks. There are five recognised species of *Paratanais* which have been described from Australia (see Larsen 2001; Bamber 2005), all of which, unlike the present species, have a two-segmented uropod endopod. *P. wanga* sp. nov. shares the lack of an 'anteriomedial' seta on the maxilliped endite only with *P. malignus* Larsen, 2001, from New South Wales. What appears to be unique to the present species is the number of blunt setae on the antennules, cheliped, etc. — while some of these may represent damage, they were a recognisable feature on all the female specimens.

Males of this genus are rare. The present male shares the body form and huge eyes noted in other species (e.g. *P. maleficus* Larsen, 2001, from New South Wales), but the flagellum segments are more numerous than in any other described male.

All of the material collected was from epifauna of algal habitats in 4–29 m depth.

<div align="center">

Family Leptocheliidae Lang 1973

Konarus Bamber, 2006

Konarus cheiris Bamber, 2006

</div>

Konarus cheiris Bamber, 2006: 7–12, figs 3–5.

Material Examined. QM-W2228111, 4 ♀♀ without oostegites sponge and bryozoan epifauna, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28112, 3 ♀♀, two within tubes in filamentous red algae, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005; NHM 2006.1560–1569 in ethanol, 11 ♀♀, eight within tubes amongst sponge, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28113, 2 ♀♀, 1 juv in *Phoronis* tube mat, Point Lookout, 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005. QM-W28114, 2 ♀♀ among the alga *Melanamansia glomerata*, Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8–15 m, 17.02.2005. QM-W28115, 8 ♀♀ among the algae *Amphiroa fragilissima*, with *Asparagopsis taxiformis* and *Zonaria diesingiana*, Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8–15 m, 17.02.2005. QM-W28116, ♀ on the bryozoan *Orthoscuticella ventricosa* agg., Henderson's Pinnacles, East side of Moreton I., 27°07.901'S, 153°28.712'E, 22–26 m, 22.02.2005. All from diving, A-NL. QM-W28472, brooding ♀, 1 manca, on medium sand with detritus and holothurians, East of Moreton I., 27°17.26'S, 153°29.141'E, 40 m, 22.02.2005, long-arm van Veen grab, RNB. QM-W28473, ♀, MBWS Stn. 9; QM-W28476,12 ♀♀, MBWS Stn. 10; van Veen grab, PJFD.

Remarks. *K. cheiris* was described originally from New Caledonia and the Loyalty Islands at 12–20 m, also on algae. These specimens are from the other side of the Coral Sea, and from 8–40 m depth. While basically white in colour, there are scarlet lines on the cheliped propodus and on the cephalon, marking the second thoracomere demarcation dorsally on the carapace (by which the genus can be easily recognised). The antennule peduncle article 1 is very robust, and the proximal end of the chela is somewhat covered by a cuff-like extension of the carpus. Some of the present material was collected in tubes of mucopolysaccharide, fibres and adherent sand grains and shell fragments.

A second species which should be transferred to this genus is *Heterotanais crassicornis* Stebbing, 1905, which was originally collected in shallow waters from the Gulf of Manaar (Stebbing 1905); this species also has the junction between the cephalon and the first thoracomere delineated on the carapace, as well as the distal cuff on the carpus of the cheliped enclosing the proximal part of the chela, and the compact antennule, after which the species was named. It seems unlikely that *H. crassicornis* Nierstrasz, 1913 is the same species, as it was collected in Pacific Indonesia at 30 m depth. Nierstrasz (1913) listed a few slight differences in size and shape which he attributed to intraspecific variation, but, as descriptions and figures for both records of *Konarus crassicornis* comb. nov. are lacking in detail, their distinction or otherwise remains inconclusive. Both forms of *K. crassicornis* have one, not two, distal setae on the maxillule palp, and less than 2 ventral setae on the fixed finger of the chela, unlike *K. cheiris*.

<div align="center">

Leptochelia Dana, 1849

Leptochelia 'savignyi' (Krøyer, 1842) complex

</div>

Remarks. The history of the *Leptochelia savignyi* (Krøyer, 1842) complex, which has included the synonymy of numerous world-wide taxa by Lang (1973), has made the distinction of the probably numerous species difficult, not least because there are very few detailed descriptions of morphology, and many taxa were described largely from the highly dimorphic males. The sex-ratio in this genus is always heavily biased towards females; for example, Bird &
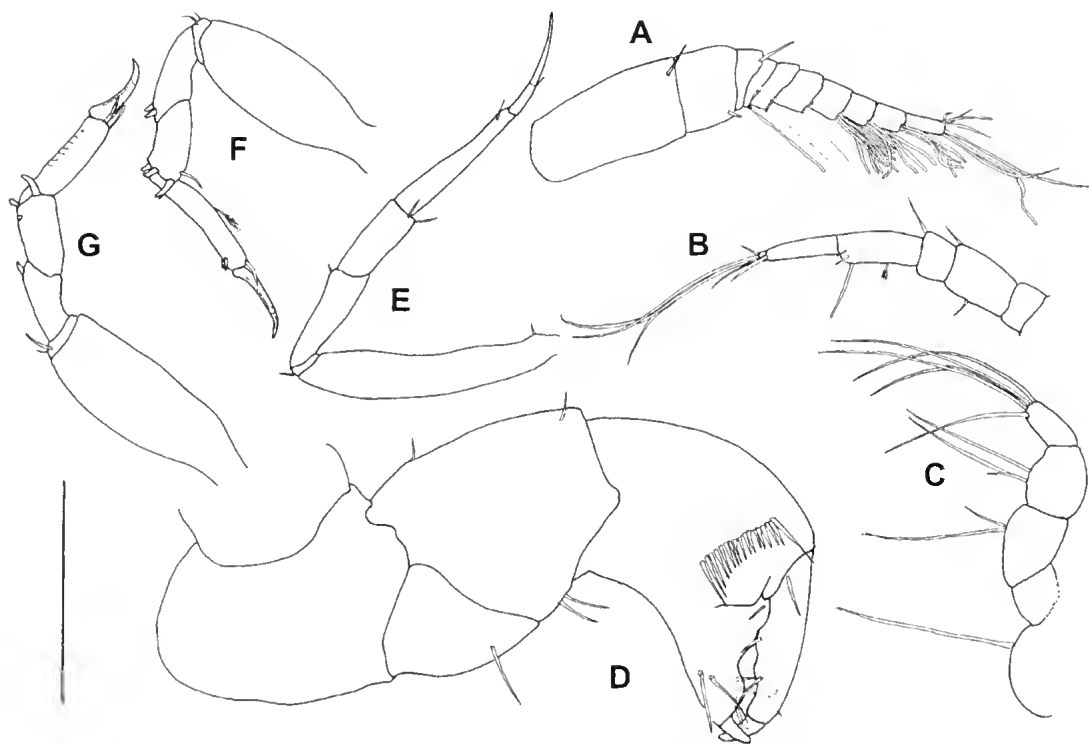
FIG. 24. *Paratanais wanga* sp. nov., male allotype, **A**, antennule (most proximal aesthetascs only indicated by their bases); **B**, antenna; **C**, maxilliped in situ; **D**, cheliped; **E**, pereopod 1; **F**, pereopod 3; **G**, pereopod 6. Scale bar = 0.4 mm for A, B, D–G; 0.2 mm for C.

Bamber (2000) recorded three males in 104 specimens of their *L.* aff. *savignyi* (non Krøyer 1842), and Ishimaru (1985) found two males in 6,500 individuals of *L. itoi* Ishimaru, 1985. Species of this group are often locally common or abundant, and it is thus necessary where possible not only to distinguish the individual taxa but also to base this distinction where possible on females. Sieg (1980) demonstrated the value of examining such detail as the spination/setation of the pereopods, *inter alia*, in the specific distinctions within the Tanaidae: such an approach has been neglected in the Leptocheliidae. A detailed redescription of *L. savignyi* s. str. from the northeastern Atlantic would be invaluable (type locality is Madeira); however, the interpretation of Sars (1886) that that species has a five-articled antennule (including the minute distal article) appears valid.

The first approach to comprehensive description was by Shiino (1965) who described '*Leptochelia savignyi*' from the Bismarck Archipelago, Melanesia. Ishimaru (1985) gave a detailed analysis of both genders of *L. itoi* and a Japanese species attributed to *L. savignyi*. Subsequently, Bird & Bamber (2000) gave a detailed analysis of distinctions between their *L.* aff. *savignyi* and *L. lusei* Bamber & Bird, 1997. Larsen & Rayment (2002) described two species of '*Leptochelia*' from the Andaman Sea, although their *L. elongata* may be inappropriate to this genus as the distal three antennule articles are subequal in length (in all other species of the genus, the distal article is minute, about 0.05 times the length of the subdistal article). Bamber (2005) described the first two Australian species attributable to *Leptochelia*, *L. nobbi* Bamber, 2005, and *L. daggi* Bamber, 2005, and presented a table comparing a range of morphological features for most species for which adequate descriptions of the females were available.

It is now apparent that, in a taxon with minimal dispersive capability, there is a large number of species of the *Leptochelia savignyi*-- complex in shallow waters around the world. Indeed, Larsen & Rayment (2002) considered

Leptochelia as 'probably the most numerically abundant shallow-water genus worldwide', with co-occurrence of cryptic species. There are known sibling species sharing sympatric distributions (Ishimaru 1985; Bird & Bamber 2000; Bamber 2005), that show niche specificity through exploitation of distinct habitats.

Characters which have so far been found to offer consistent distinctions between females of the species include the dimensions of the antennule proximal article; setation of the pereopod 1 carpus, the antennules and antennae; the proportions of the pereopod articles (particularly merus:carpus ratios of pereopods 2 and 3); the spination of the pereopod 2/3 merus; the maxilliped basis setae and endite spines; the proportions of the cheliped basis and carpus; the uropod exopod and possibly the lacinia mobilis of the left mandible. Observation of live material has also found colour differences between species, but many of the taxa *in litt.* are known only from preserved material, which has lost its pigmentation. Male morphology (when available) often offers early indication of specific differences.

A number of species of *Leptochelia* were collected in the range of habitats around Moreton Bay. They have been analysed in comparison with the data presented by Bamber (2005, Table 1) covering the eight taxa listed therein, plus *L. dubia* Sars, 1886, *L. neapolitana* Sars, 1886, *L. nobbi*, *L. daggi*, and *L. tarda* Larsen & Rayment, 2002. The Brazilian taxon *L. dubia* (Krøyer, 1842) (non *L. dubia* Dojiri & Sieg, 1977) cannot be included as the description of that species is inadequate; similarly, insufficient detail is available for *L. savignyi sensu* Krøyer, 1842, and that species appears to have a five-articled antennule, as does *L. savignyi sensu* Sars, 1886, making them quite distinct from the remaining taxa (see *Catenarius* gen. nov., below).

Leptochelia myora sp. nov.
(Figs 25, 26)

Material Examined. HOLOTYPE: QM-W28117, ♀ with oostegites, QM-W28118, 11 ♀♀. PARATYPES: QM-W28119, ♂, allotype, ♂ with oostegites, dissected, *Zostera capricorni* bed on soft sand, beach off Myora Spring, North Stradbroke I., 27°28.2'S, 153°25.45'E, mid-littoral (trowel sample), 32‰, 9.02.2005, RNB.

Description of Female. Body (Fig. 25A) slender, holotype 2 mm long, 7.3 times as long as wide.

Cephalothorax subrectangular, 1.6 times as long as wide, longer than pereonites 1 and 2 together, with slight rostrum, eyelobes prominent, eyes present and black. Six free pereonites; pereonites 1, 2, 3, 5 and 6 subequal in length, pereonite 4 longest, 1.3 times as long as pereonite 1 (all pereonites respectively 1.6, 1.4, 1.5, 1.1, 1.3 and 1.6 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; pleon just longer than cephalon, each pleonite about 3.6 times as wide as long. Pleotelson semicircular, longer than last two pleonites together, twice as wide as long, with one posterolateral seta on each side and two distal setae. Body live colour generally brown with scattered white patches.

Antennule (Fig. 25C) of four tapering articles, proximal article 2.64 times as long as wide, 1.25 times as long as distal three articles together, with two long outer and single long inner setae; second article 1.8 times as long as wide, 0.4 times as long as first, distal setae half length of article; third article just shorter than second, with one aesthetasc; fourth article minute, eccentric, with four distal setae.

Antenna (Fig. 25E) of six articles, proximal article compact, naked; second article as long as wide, with single ventrodistal and dorsodistal slender spines; third article as long as wide, with dorsodistal spine; fourth article longest, 2.9 times as long as wide; fifth article 0.6 times as long as fourth; sixth article minute.

Labrum (not figured) rounded, setose, typical of genus. Left mandible (Fig. 25G) with crenulate lacinia mobilis tapering towards distal end of mandible, coarse crenulation on pars incisiva, pars molaris stout; right mandible (Fig. 25F) with long crenulate margin, without lacinia mobilis. Labium (not figured) wide, distally finely setose, without palp. Maxillule (Fig. 25J) with ten distal spines and setose margins; palp distinct, with two distal setae. Maxilliped (Fig. 25H) palp first article naked, second article with finely setose inner margin, and with one outer and four inner setae, distal-most inner seta almost reaching distal margin of third palp article; third and fourth articles with filtering rows of ten and eight setae respectively, third article with three further outer setae, fourth article with outer seta; basis (Fig. 25I) with four long setae extending to third palp article; endites

distally with single seta and two robust spatulate and one rounded spines. Maxilla (not figured) oval, naked; epignath (not figured) elongate with setose margin distally and proximally.

Cheliped (Fig. 25K) with rounded, compact basis 1.3 times as long as wide; merus subtriangular with three ventral setae; carpus twice as long as wide, with three midventral and one subdistal dorsal setae; propodus typical for the genus, fixed finger with three ventral and three inner setae, cutting edge hardly crenulate, setal row at base of dactylus of three setae; dactylus with dorsoproximal seta.

Pereopod 1 (Fig. 26B) longer than other pereopods, coxa with seta; basis slender, 2.6 times as long as wide; ischium compact with one seta; merus as long as carpus, naked; carpus with three short distal setae, longest of which is 0.17 times length of propodus; propodus longer than carpus and merus together, with three longer dorsodistal setae on distinct raised pad; dactylus slender, extending into shorter slender unguis, the two together some 1.26 times as long as propodus.

Pereopod 2 (Fig. 26C) more compact than pereopod 1; ischium with one seta; merus just shorter than carpus, merus with strong ventrodistal spine and dorsodistal seta, carpus with single dorsodistal and ventrodistal setae; propodus shorter than carpus and merus together, with three longer dorsodistal setae on distinct raised pad; dactylus and shorter unguis together as long as propodus.

Pereopod 3 (Fig. 26D) similar to pereopod 2, but merus without dorsodistal seta, carpus with short outer distal spine, dactylus plus unguis 0.75 times as long as propodus.

Pereopod 4 (Fig. 26E) basis stout, twice as long as wide; ischium with one seta; merus and carpus subequal; merus with one outer and one inner short, ventrodistal tooth-like spine; carpus with two outer and one inner distal tooth-like spines and fine dorsodistal seta; propodus longer than carpus, with two dorsodistal setae longer than dactylus, one shorter subdistal dorsal seta, one ventral subdistal tooth-like spine and one outer distal tooth-like spine; dactylus and unguis partially fused, curved. Pereopod 5 as pereopod 4. Pereopod 6 (Fig. 26F) as pereopod 4, but propodus with paired ventral subdistal spines and no outer distal spine, dorsodistally with two pectinate and three simple setae.

Pleopods all alike, typical for the genus, basis naked.

Uropod (Fig. 26G) biramous, basis naked; exopod of one segment, 0.5 times as long as proximal endopod segment, outer distal seta longer than inner distal seta; endopod of four segments, distal segments slender.

Description of Male. Highly dimorphic primary male, smaller than female (allotype length 1.5 mm), body more compact; cephalon (Fig. 25B) elongate, nearly twice as long as wide, tapering towards rostrum, longer than pereonites 1–3 together, with distinct eyelobes bearing black eyes; pereonite 1 shortest, most pereonites subequal, pereonite 5 longest, 1.4 times as long as pereonite 1. Five free pleonites, subequal in length, entire pleon twice as long as pereonite 1. Sexual dimorphism as follows.

Antennule (Fig. 25D) elongate, slender, of 6 articles; first peduncle article 4 times as long as wide with one shorter and one longer distal setae, the latter almost as long as second article; second article half as long as first; third to sixth articles bearing 3, 3, 5 and 7 distal aesthetascs respectively. Mouthparts atrophied.

Cheliped (Fig. 26A) highly modified, more robust than that of female; basis as long as wide; carpus with convex dorsal edge and ventral flange, the whole thus being almost as wide as long; propodus with setal row at base of dactylus of 14 setae. Fixed finger set at right-angles to axis of propodus, 1.25 times as long as propodus, with large tooth-like apophysis on cutting edge bearing three setae; dactylus as long as fixed finger, but tips not opposing, cutting edge with four small spines.

Pleopods more setose than those of female.

Female to male sex ratio of the type material is 13:1.

Etymology. Named after the mangrove spring at the type locality.

Remarks. With the uropod exopod only half the length of the first endopod segment, *L. myora* sp. nov. compares only with *L. neapolitana* Sars, 1886, from the Mediterranean, *L. nobbi* from southwestern Australia, and *L. lusei* Bamber & Bird, 1997 (0.6 times); the latter two species
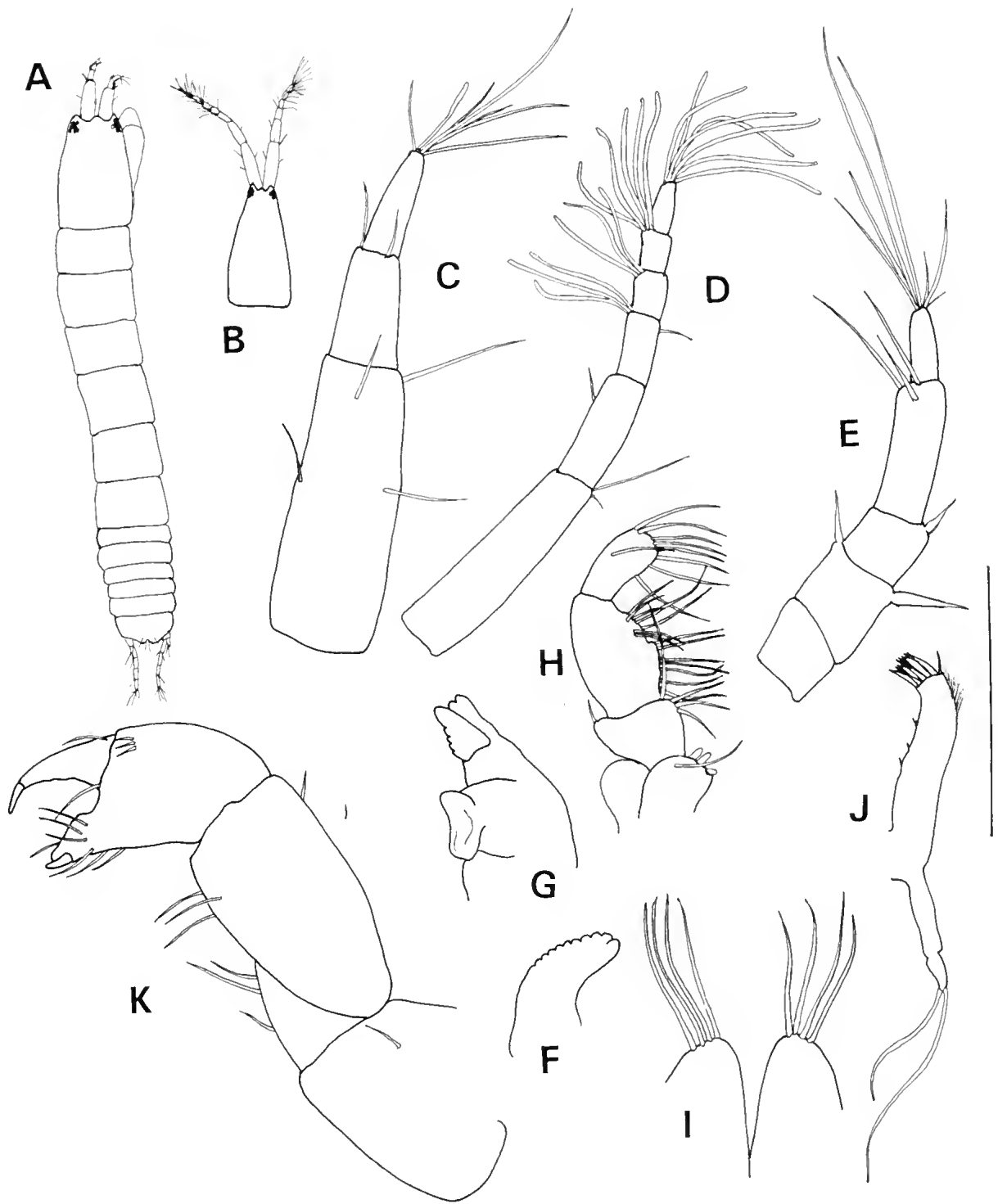
FIG. 25. *Leptochelia myora* sp. nov., **A**, female holotype, dorsal; **B**, cephalon and antennules of male allotype, dorsal; **C**, female antennule; **D**, male antennule; **E**, antenna; **F**, right mandible, distal; **G**, left mandible; **H**, maxilliped palp and endite; **I**; maxilliped bases; **J**, maxillule; **K**, female cheliped. Scale bar = 1 mm for A, B; 0.25 mm for C, D, E; 0.2 mm for F–J; 0.35 mm for K.
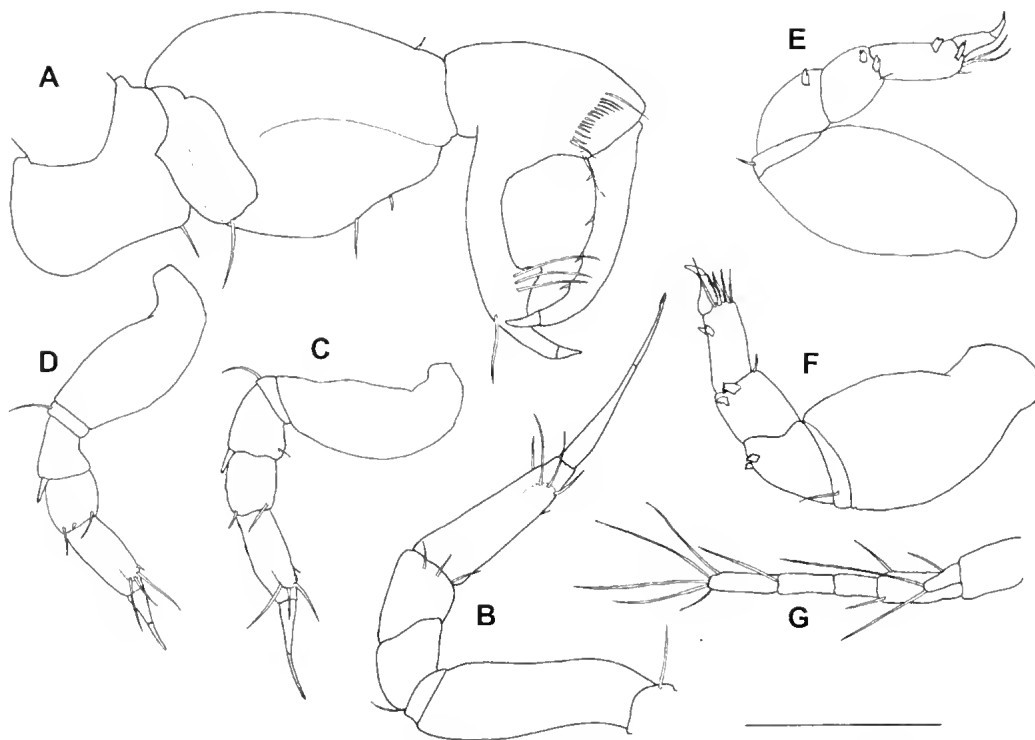
FIG. 26. *Leptochelia myora* sp. nov., **A**, male cheliped; **B–F**, pereopods 1, 2, 3, 4 and 6 respectively; **G**, uropod. Scale bar = 0.2 mm.

have only three distal setae on the maxilliped basis, compared with four in *L. myora*; *L. neapolitana* has five. The cephalon of *L. myora* is proportionately longer (1.6 times as long as wide) than *L. neapolitana* (1.3 times) *L. nobbi* (1.15 times) or *L. lusei* (1.4 times). The basis of pereopod 1 in the present species is proportionately shorter (2.6 times its own width) than in any other species of this group, all of which have the basis at least 3 times as long as its own width. The longest distal seta on the carpus of pereopod 1 (0.17 times the length of the propodus) is shorter than in any other species (at least 0.3 times the length of the propodus), and the longest distal seta on article 2 of the antennule (0.6 times as long as the article) is also shortest in this species (0.64 in *L.* aff. *savignyi* Bird & Bamber, 2000; >0,8 times in all other species). *L. myora* is further distinct from the two previously described Australian species in having two spatulate and one low rounded distal spines on the maxilliped endite, both *L. nobbi* and *L. daggi* Bamber, 2005 having three spatulate spines.

The raised dorsodistal pad bearing setae on the propodus of pereopods 1–3 of the present species, while probably present in all other species of *Leptochelia*, is most conspicuous in *L. myora*.

The male of the present species is distinct from those of the other species in the *Leptochelia savignyi* aggregate. In particular, the elaborate carpus is unique.

Leptochelia dijonesae sp. nov.
(Figs 27–29)

FIG. 27. *Leptochelia dijonesae* sp. nov., **A**, holotype female, dorsal; **B**, allotype male, dorsal; **C**, antennules; **D**, antenna; **E**, pars incisiva of right mandible; **F**, left mandible; **G**, maxillule endite; **H**, maxilliped; **I**, uropod of 1.14 mm manca; **J**, uropod of 2.13 mm female; **K**, uropod of 3.9 mm female with oostegites. Scale bar = 1 mm for A, B; 0.3 mm for C, D; 0.2 mm for E–H; 0.15 mm for I–K.

Description of Female. Body (Fig. 27A) slender, holotype 3.9 mm long, 7 times as long as wide. Cephalothorax subrectangular, 1.3 times as long as wide, 1.3 times as long as pereonites 1 and 2 together, with blunt rostrum, eyelobes conspicuous, eyes present and black, single setae at posterior of eyelobes. Six free pereonites; pereonite 1 shortest, pereonites 2, 3 and 4 progres-
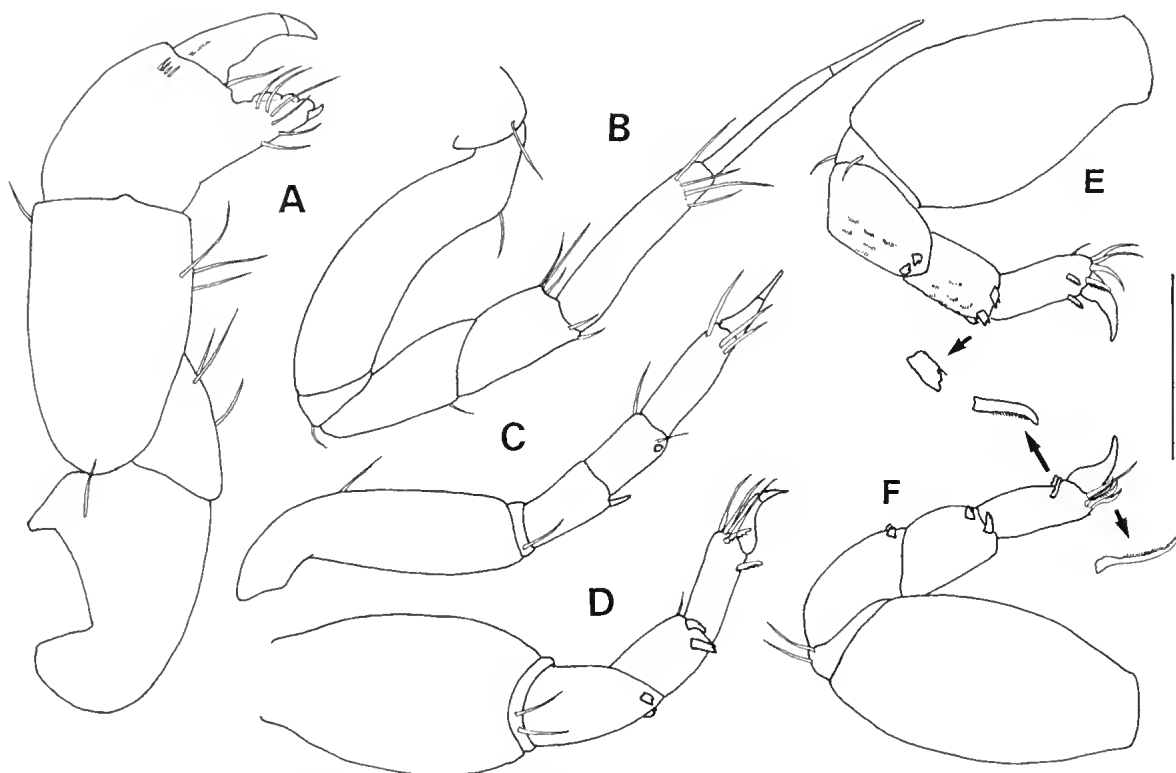
FIG. 28. *Leptochelia dijonesae* sp. nov., female paratype, **A**, cheliped; **B–F**, pereopods 1, 2, 4, 5 and 6 respectively. Scale bar = 0.3 mm for A; 0.2 mm for B–F.

sively longer, pereonite 5 just shorter than pereonite 4, pereonite 6 as long as pereonite 2 (all pereonites respectively 2.6, 1.7, 1.4, 1.2, 1.3 and 1.8 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 4.5 times as wide as long, with dorsal setal pair on last three pleonites. Pleotelson semicircular, as long as last two pleonites together, twice as wide as long, with one anterodorsal and one posterolateral setae on each side and two distal setae. Body live colouration olive green.

Antennule (Fig. 27C) of four tapering articles, proximal article 2.9 times as long as wide, 1.5 times as long as distal three articles together, with two outer setae at midlength, three outer distal setae (longest of these 1.5 times length of article 2), and single inner seta at midlength; second article 1.5 times as long as wide, one third length of proximal article, longest distal seta 0.8 times length of article; third article just shorter than second, with one aesthetasc; fourth article minute, with three distal setae.

Antenna (Fig. 27D) of six articles, proximal article compact, naked; second article as long as wide, with single ventrodistal and dorsodistal slender spines; third article as long as wide, with dorsodistal slender spine; fourth article longest, 4 times as long as wide; fifth article 0.5 times as long as fourth; sixth article minute.

Labrum rounded, setose, typical of genus. Left mandible (Fig. 27F) with crenulate lacinia mobilis longer than distal end of mandible, proximal crenulation on pars incisiva, pars molaris with strong rugosity; right mandible (Fig. 27E) similar but without lacinia mobilis, pars incisiva with more crenulations. Labium (not figured) wide, distally finely setose, without palp. Maxillule (Fig. 27G) with ten distal spines and setose margins, single row of setules on inner distal face, sparser single setae along ventral margin; palp (not figured) distinct, with two distal setae. Maxilliped (Fig. 27H) palp first article naked, second article with one outer and three inner setae, single distal seta almost reaching distal margin of third palp article; third and fourth
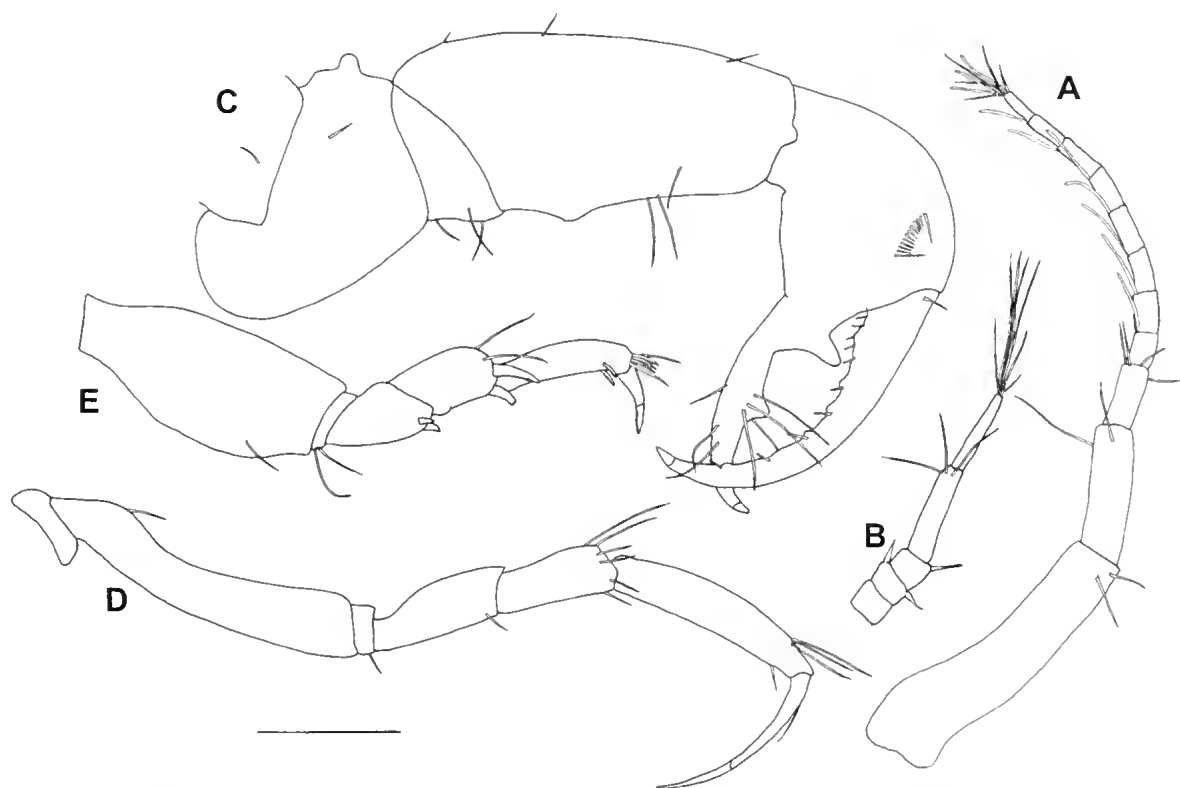
FIG. 29. *Leptochelia dijonesae* sp. nov., male paratype, **A**, antennule; **B**, antenna; **C**, cheliped; **D**, pereopod 1; E. pereopod 6. Scale bar = 0.3 mm for A, B, C; 0.2 mm for D, E.

articles with filtering rows of nine and seven setae respectively, fourth article with additional outer seta; basis with four or five long setae (including in same specimen) extending to mid-length of third palp article; endites distally with single finely setulose seta and two spatulate and one inner rounded blunt spines. Maxilla (not figured) oval, naked; epignath (not figured) elongate with setose margins.

Cheliped (Fig. 28A) with rounded, compact basis 1.35 times as long as wide; merus subtriangular with three ventral setae; carpus 1.73 times as long as wide, with three midventral setae; propodus typical for the genus, fixed finger with two ventral, one lateral and three inner setae, cutting edge with three plate-like teeth, setal row at base of dactylus of four setae; dactylus with proximal outer seta.

Pereopod 1 (Fig. 28B) longer than other pereopods, coxa with seta; basis slender, 3.73 times as long as wide; ischium compact with one seta; merus just longer than carpus, with single ventro-distal seta; carpus with three dorsodistal and two ventrodistal setae, longest of which is 0.4 times length of propodus; propodus nearly twice as long as carpus, with four distal setae on slight raised pad; dactylus slender, extending into shorter slender unguis, the two together some 1.28 times as long as propodus.

Pereopod 2 (Fig. 28C) more compact than pereopod 1; basis 3 times as long as wide; ischium with one ventrodistal seta; merus longer than carpus, merus with strong ventrodistal spine, carpus with dorsodistal seta; dactylus and short unguis together 0.75 times as long as propodus. Pereopod 3 (not figured) similar to pereopod 2, carpus shorter than merus, but ischium with two ventrodistal setae.

Pereopod 4 (Fig. 28D) basis stout, 1.6 times as long as wide; ischium with two setae; merus 1.5 times as long as carpus; merus with paired short, ventrodistal tooth-like spines; carpus with one outer, one ventral and one inner distal spines each with fine outer setule; propodus longer

than carpus, with three distal slender simple setae as long as dactylus plus unguis, single inner-distal and ventrodistal denticulate spines; dactylus and unguis shaped but not fused into an unguis, curved. Pereopod 5 (Fig. 28E) as pereopod 4, but with dorsal subdistal fine seta and additional inner subdistal denticulate spine. Pereopod 6 (Fig. 28F) as pereopod 4, but propodus with paired ventrodistal denticulate spines and four pectinate and one simple dorsodistal setae.

Pleopods all alike, typical for the genus, with single pleopods 1–3) or no (4 and 5) dorsal plumose seta on basis.

Uropod (Fig. 27K) biramous, basis naked; exopod of two segments, 1.4 times as long as proximal endopod segment, outer distal seta shorter than inner distal seta, proximal segment with short outer seta; endopod of five slender segments, distal three segments longer than proximal pair. Uropod of manca (Fig. 27I) exopod 1-segmented, endopod 3-segmented; uropod of subadult female (Fig. 27J) exopod 1-segmented, endopod 4-segmented.

Description of Male. Typical secondary male, shorter than female (allotype length 3.0 mm), body (Fig. 27B) more compact, 4.2 times as long as wide, cephalon longer than pereonites 1–3 together, with large eyelobes bearing large black eyes; pereonite 1 shortest, pereonites 2, 3 and 4 progressively longer, pereonite 5 just shorter than pereonite 4, pereonite 6 as long as pereonite 2. Five free pleonites, subequal in length, pleon in total as long as cephalon, pleotelson just longer than pleonites 4 and 5 together. Sexual dimorphism as follows.

Antennule (Fig. 29A) elongate, first peduncle article 3.7 times as long as wide with 2 dorsodistal setae; second article 0.46 times as long as first with long ventrodistal setae; third article half length of second; flagellum of 8 segments, distal article with three aesthetascs, all others with single distal aesthetasc. Antennule (Fig. 29B) more slender, fifth article almost as long as fourth. Mouthparts atrophied.

Cheliped (Fig. 29C) more robust than that of female; basis 1.2 times as long as wide with dorsodistal rounded apophysis; carpus 1.8 times as long as wide with sparse dorsal marginal setae; propodus fixed finger longer than palm,

with two inner tooth-like apophyses on cutting edge, distal apophysis with three long adjacent setae; moveable finger recurved with series of short setae along cutting edge; setal row at base of dactylus with twelve setae.

Pereopods more slender than those of female; pereopod 1 (Fig. 29D) basis five times as long as wide, dactylus plus unguis shorter than propodus. Posterior pereopods (e.g. Fig. 29E) with larger distal spines on carpus,

Pleopods more setose than those of female. Uropods similar to those of female but basis with six distal setae.

Female to male sex ratio over all the material is 9.5:1

Etymology. Named for Dr Diana Jones of the Western Australia Museum, Perth, who collected the type series.

Remarks. *Leptochelia dijonesae* sp. nov. is the only species of the *L. savignyi*–complex to have a 2-segmented uropod exopod (some species of the sibling genera *Pseudoleptochelia* Lang, 1973, *Pseudonototanais* Lang, 1973, and *Catenarius*, newly erected below, also have a two-articled exopod). The exopod is also far longer in proportion to the proximal endopod article (1.4 times as long) than any other taxon (1.1 times as long in *L. daggi*, otherwise shorter). With *L. daggi* only it shares the character of the carpus of pereopods 2 and 3 being shorter than the merus. However, the cheliped carpus is shorter in proportion to its width (1.73 times as long) than in any other species (*L. savignyi sensu* Ishimaru, 1985, 1.85 times as long; all others >1.9 times as long). The secondary male of the present species bears many similarities to that of the West Australian species *L. daggi*, but again is distinguished by the 2-segmented uropod endopod.

Leptochelia opteros sp. nov.
(Figs 30–32)

Material Examined. HOLOTYPE: QM-W28125, brooding ♀, QM-W28126, ♂ allotype. PARATYPES: QM-W28127, 5 ♂♂, 22 ♀♀ (5 brooding), 6 juvs/mancae. NHM 2006.1576–1581, 2 ♂♂, 2 ♀♀, 2 mancae, amongst filamentous red algae, Point Lookout, North Stradbroke I., 27°26.31′S, 153°32.52′E, 10 m, 12.02.2005, diver A-NL. QM-W28128, 2 ♂♂, 27 ♀♀ (5 brooding), 3 juvs/mancae. NHM 2006.1582–1620, 6 ♂♂, 29 ♀♀ (8 brooding), 4 juvs/mancae, amongst *Cladophoropsis vaucheriaeformis*, low shore at Amity Point, North

Stradbroke I., 27°23.9'S, 153°26.2'E, +0.5 m CD, 20.02.2005, A-NL. QM-W28129, 5 ♂♂, 78 ♀♀ (14 brooding), 13 juvs/mancae, amongst sponges, Shag Rock, north of North Stradbroke I., 27°24.8'S, 153° 31.5'E, 15 m, 15.02.2005, A-NL. QM-W28130, 3 ♀♀ (1 brooding), 1 manca, amongst haploslerid sponges, Shag Rock, north of North Stradbroke I., 27°24.8'S, 153°31.5'E, 18 m, 15.02.2005, J.Carini. QM-W28131, 2 ♀♀, 1 manca, amongst haploslerid sponge, Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8 m, 17.02.2005, J Carini. 1 subadult, sandy mud with some seagrass, NE of Banana Bank, Moreton Bay, 27°32.46'S, 153 °20.74'E, 3.1 m, 33‰, 28°C, 17.02.2005, both van Veen grab, RNB. QM-W28132, 2 ♀♀, 1 manca, amongst algae (*Amphiroa fragilissima*, *Asparagopsis taxiformis* and *Zonaria diesingiana*), Flat Rock, north of North Stradbroke I., 27°23.5'S, 153°33.0'E, 8–15 m, 17.02.2005, A-NL. QM-W28133, 3 ♀♀ (2 brooding), 3 juvs/mancae, amongst *Cladophoropsis vaucheriaeformis*, Amity Point, North Stradbroke I., 27°23.9'S, 153°26.2'E, 5–10 m, 14.02.2005, A-NL. QM-W28134, 2 ♀♀ (1 brooding), 1 manca, amongst sponges with ascidians, Amity Point, North Stradbroke I., 27°23.9'S, 153°26.2'E, 5–10 m, 14.02.2005, A-NL. QM-W28135, ♂ (red), 12 ♀♀, 3 juvs/mancae, amongst barnacle-sponge epifaunal on tyres, off Amity Point, North Stradbroke I., 27° 23.9'S, 153°26.2'E, 8–10 m, 35‰, 14.02.2005, A-NL. NHM 2006.1621–1629, ♂, 7 ♀♀ (2 brooding), 1 juv. amongst empty *Phoronis* tubes, Point Lookout, North Stradbroke I., 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005, A-NL. NHM 2006.1630–1648, ♂, 11 ♀♀ (2 brooding), 7 juvs/mancae, amongst sponge and bryozoan epifauna, Point Lookout, North Stradbroke I., 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005, A-NL. QM-W28136, 3 ♂♂, 3 ♀♀, 13 juvs/mancae, littoral open sand, Bradbury Beach, Dunwich, North Stradbroke I., 27°29.6'S, 153°23.8'E, 13.02.2005, RNB. QM-W28137, 2 ♀♀, amongst zosteretum with *Halophila ovalis*, inside Amity Point sand bar, North Stradbroke I., 27°24.7'S, 153° 26.15'E, ELWM, 35.5‰,14.02.2005, RNB. QM-W28448, ♀, MBWS Stn. 9; QM-W28449, ♀, MBWS Stn. 13; QM-W28450, ♀, MBWS Stn. 15, all van Veen grab, PJFD. OTHER MATERIAL. QM-W28168, 9 ♀♀, Middle Banks, northern Moreton Bay, 17.09.1983/ 13.01.1984, P. Saenger & S. Cook (there are two dates on the label, in material containing a number of species). QM-W12543, 3 ♂♂, Middle Banks, northern Moreton Bay, 09.1983/1984, P. Saenger & S.Cook (there are two dates on the label). QM-W12011, 2 ♀♀, Serpentine Creek, Cribb I., Nudgee Beach, intertidal, I.Stejskal, 1984.

Description of Female. Body (Fig. 30A) slender, holotype 3.4 mm long, 6.3 times as long as wide. Cephalothorax subrectangular, laterally slightly convex, 1.3 times as long as wide, 1.3 times as long as pereonites 1 and 2 together, with slight rostrum, eyelobes and black eyes present, single setae at posterior of eyelobes. Six free pereonites; pereonite 1 shortest, pereonites 2 and 6 subequal and 1.5 times as long as pereonite 1, pereonites 3, 4 and 5 subequal and twice as long as pereonite 1 (all pereonites respectively 2.7, 1.9, 1.4, 1.3, 1.2 and 1.6 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 5 times as wide as long. Pleotelson semicircular, as long as last two pleonites together, almost twice as wide as long, with two posterolateral setae and two distal setae on each side.

Antennule (Fig. 30C) of four tapering articles, proximal article 2.6 times as long as wide, 1.35 times as long as distal three articles together, with two long outer and two shorter inner/dorsal setae, outer distal seta much longer than second article; second article 1.5 times as long as wide, distal outer seta as long as article; third article just shorter than second, with four distal setae and one aesthetasc; fourth article minute, eccentric, with three distal setae.

Antenna (Fig. 30D) of six articles, proximal article compact with ventrodistal seta; second article as long as wide, with single inner distal and dorsodistal slender spines; third article as long as wide, with dorsodistal slender spine; fourth article longest, 3.7 times as long as wide; fifth article 0.4 times as long as fourth; sixth article minute.

Labrum rounded, setose, typical of genus. Left mandible (Fig. 30G) with crenulate lacinia mobilis as wide as distal end of mandible, proximal crenulation on pars incisiva, pars molaris with strong rugosity and marginal spines; right mandible similar but without lacinia mobilis. Labium (not figured) wide, distally finely setose, without palp. Maxillule (Fig. 30E) with ten distal spines and setose margins, sparse row of setules on inner distal face, sparser and paired setae along ventral margin; palp distinct, with two distal setae. Maxilliped palp (Fig. 30F) first article naked, second article with one outer and four inner setae, distal-most inner seta reaching distal margin of third palp article; third and fourth articles with filtering rows of seven and nine setae respectively, third article with two further inner distal setae, fourth article with outer seta; basis with four long setae extending to third palp article; endites distally with single seta and two robust spatulate and one rounded spines. Maxilla (not figured) oval, naked; epignath
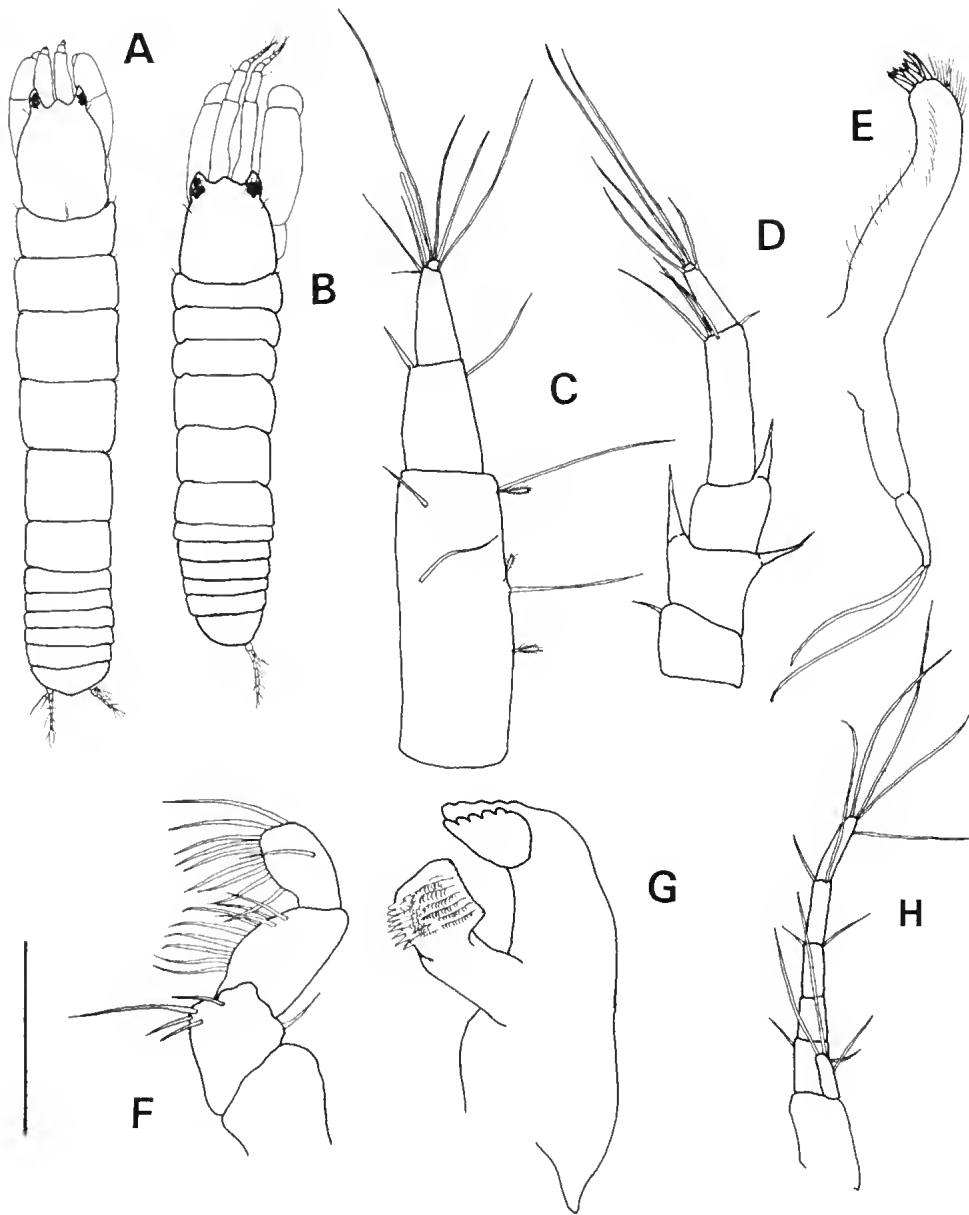
FIG. 30. *Leptochelia opteros* sp. nov., **A**, holotype female, dorsal; **B**, allotype male, dorsal; **C**, female antennule; **D**, female antenna; **E**, maxillule; **F**, maxilliped palp; **G**, left mandible; **H**, uropod. Scale bar = 1 mm for A, B; 0.2 mm for C, D, H; 0.1 mm for E, F, G.

(not figured) elongate with setose margin distally and proximally.

Cheliped (Fig. 31A) with rounded, compact basis 1.2 times as long as wide wide; merus subtriangular with three ventral setae; carpus 1.6 times as long as wide, with three ventrodistal setae; propodus typical for the genus, fixed finger with three ventral, one outer and three inner setae, cutting edge with three plate-like teeth, setal row at base of dactylus of six setae; dactylus naked.

Pereopod 1 (Fig. 31B) longer than other pereopods, coxa with seta; basis slender, 4.5 times as long as wide; ischium compact with one seta;
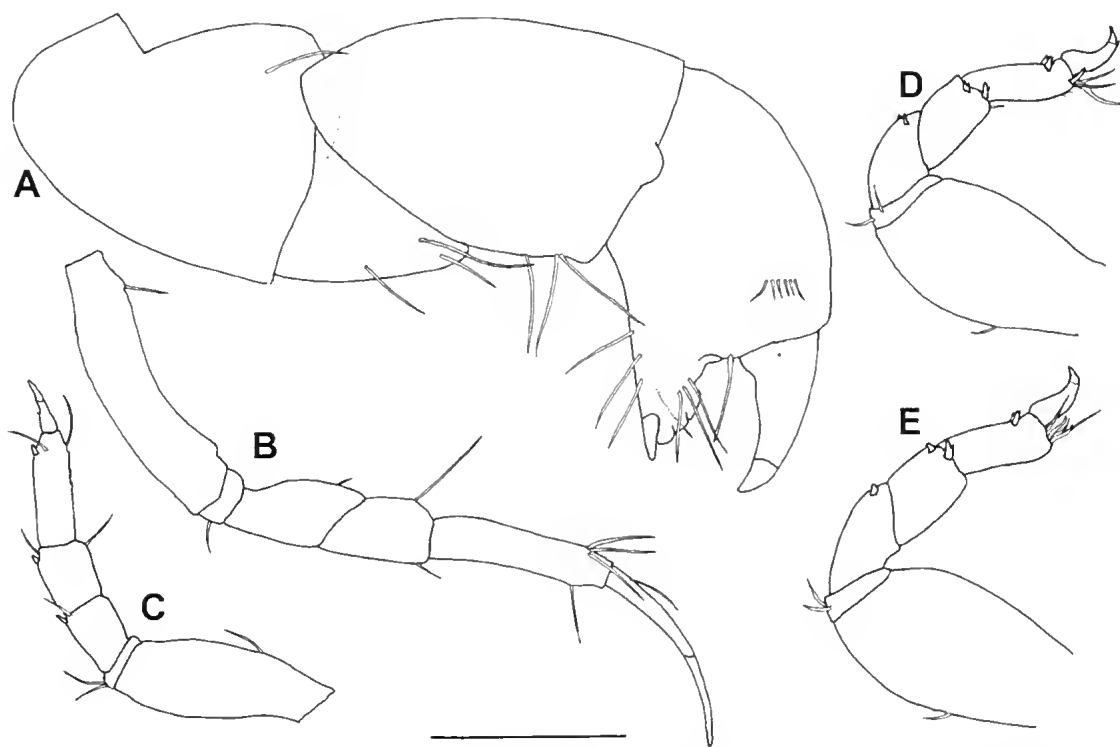
FIG. 31. *Leptochelia opteros* sp. nov., female, **A**, cheliped; **B**, pereopod 1; **C**, pereopod 3; **D**, pereopod 4; **E**, pereopod 6. Scale bar = 0.2 mm.

merus just longer than carpus, with single dorso-distal seta; carpus with one long subdistal dorsal seta half length of propodus and one short ventrodistal seta; propodus as long as carpus and merus together, with ventral sub-distal seta and three dorsodistal setae; dactylus slender, extending into shorter slender unguis, the two together some 1.1 times as long as pro-podus; single proximal seta on dactylus. Pereo-pods 2 and 3 (Fig. 31C) similar to each other, more compact than pereopod 1; ischium with 2 setae; merus as long as carpus, merus with short ventrodistal spine and adjacent seta, carpus with ventrodistal spine and adjacent seta and dorso-distal seta; propodus 1.8 times as long as carpus with ventrodistal spine; dactylus and short unguis together 0.5 times as long as propodus.

Pereopods 4 (Fig. 31D) and 5 similar to each other, basis stout, less than twice as long as wide with single midventral seta; ischium with two setae; merus and carpus subequal, merus with two short, opposing ventrodistal spines, carpus with two anterior and one posterior distal spines each with fine outer setule; propodus longer than carpus, with one dorsodistal finely serrated spine and two ventrodistal spines with fine outer setule, three dorsodistal setae almost as long as dactylus; dactylus and unguis par-tially fused into claw, curved. Pereopod 6 (Fig. 31E) as pereopod 4, but propodus without dorso-distal spine, with three pectinate and two simple distal setae.

Pleopods all alike, typical for the genus, with single dorsal plumose seta on basis.

Uropod (Fig. 30H) biramous, basis naked; exopod of one segment, 0.8 times as long as proximal endopod segment, with median outer seta and outer distal seta longer than inner distal seta; endopod of five segments, distal segments slender.

Description of Male. Smaller than female (allo-type length 2.6 mm), body (Fig. 30B) more compact, cephalon longer than pereonites 1–3, with large eyelobes bearing large black eyes; pereonite 1 shortest, pereonites 2, 3 and 6 sub-equal, 1.5 times as long as pereonite 1; pereo-nites 4 and 5 longest, twice as long as pereonite
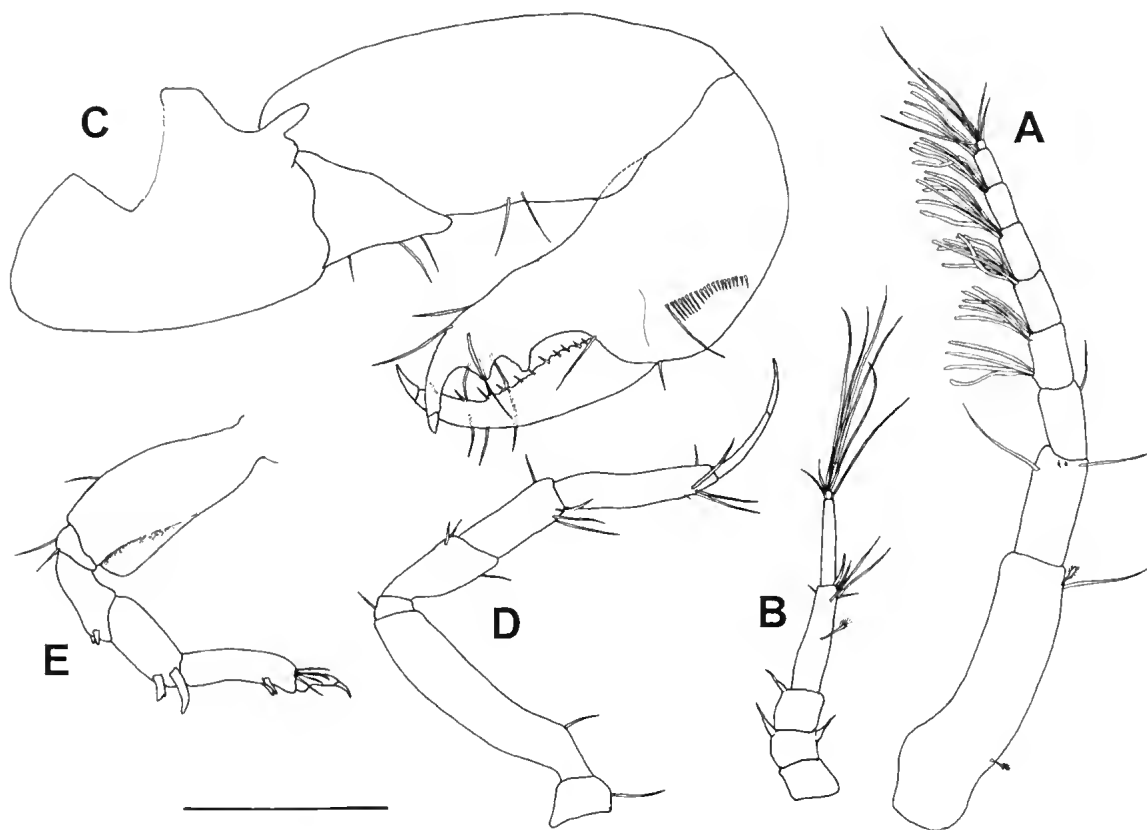
FIG. 32. *Leptochelia opteros* sp. nov., male: **A**, antennule; **B**, antenna; **C**, cheliped; **D**, pereopod 1; **E**, pereopod 6. Scale bar = 0.3 mm.

1. Five free pleonites, subequal in length, 0.6 times as long as pereonite 1, pleotelson twice as long as pleonite 5. Males on red algae and amongst epifauna red, those on *Cladophoropsis* or open littoral sand blue (colour lost on preservation). Sexual dimorphism as follows.

Antennule (Fig. 32A) elongate, first peduncle article 4 times as long as wide with dorsodistal seta longer than article width; second article 0.36 times as long as first with ventrodistal and dorsodistal seta longer than article width; third article 0.75 times as long as second; flagellum of 6 segments, first segment with proximal tuft of 4 and distal tuft of 5 aesthetascs; second to sixth articles with distal tufts of 6, 6, 4 and 3 aesthetascs respectively; distal article with single aesthetasc and 5 setae. Antenna (Fig. 32B) more slender than that of female, fifth article 0.8 times as long as fourth. Mouthparts atrophied.

Cheliped (Fig. 32C) more robust than that of female; basis nearly twice as long as wide with

dorsodistal rounded apophysis projecting past carpus base; carpus with ventrodistal invagination to accommodate propodus on reflexion; propodus setal row at base of dactylus of twenty setae; fixed finger shorter than palm, with two inner tooth-like apophyses on cutting edge; dactylus (moveable finger) with short setae and crenulations along whole of cutting edge.

Pereopods more slender than those of female, pereopod 1 (Fig. 32D) dactylus plus unguis shorter than propodus. Anterior distal spines on carpus of pereopods 4–6 (e.g. Fig. 32E) much longer than those of female; pereopod 6 (Fig. 32E) basis with conspicuous posterodorsal flange widening distally (rarely also present on pereopod 5).

Pleopod rami more setose than those of female. Uropods similar to those of female.

Female to male sex ratio over all the material is 8.7:1.

Etymology. Named for Point Lookout, the type locality (from the Greek, *opteros*, a scout or spy). Used as a noun in apposition.

Remarks. The female of *Leptochelia opteros* sp. nov. is less distinguished morphologically than the previous two species. It is distinct from *L. dijonesae* owing to its one-articled uropod exopod, and from *L. myora* (and most other described taxa) owing to the more slender pereopod 1 basis (4.5 times as long as wide compared with 2.5 times in *L. myora*), the less slender cheliped articles and the proportionately shorter dactylus plus claw on pereopod 1. The males of *L. myora* and *L. opteros* are markedly different. Of the remaining described taxa with four distal setae on the maxilliped basis, it is closest to the southwestern Australian species *L. daggi* (pereopod 1 basis 4.6 times as long as wide) with which species only it shares the longest distal seta on the carpus of pereopod 1 being half or more the length of the propodus (less than 0.45 times in the other taxa; half as long in *L. lusei*, but that species has only three maxilliped basis setae). However, the uropod exopod of *L. daggi* is longer than the proximal endopod segment (shorter in the present species), the cheliped carpus is more slender (twice as long as wide, only 1.6 times as long as wide in the present species), and the dactylus plus claw on pereopod 1 is much longer than the propodus (1.25 times as long in *L. daggi*; 1.1 times as long in *L. opteros*). None of these other species has a seta on the proximal article of the antenna, although *L. dubia sensu* Sars, 1886 and *L. neapolitana* do.

The males of *L. daggi* and *L. opteros* are also similar, but the posterodorsal flange on the basis of the rear pereopods is unique to *L. opteros* (allowing easy identification of populations where males are present). The setation of the fixed finger of the chela is less in *L. daggi*, although that species shares the distal invagination on the cheliped carpus into which the chela fits on reflexion.

Leptochelia opteros was collected from sublittoral algae and epifaunal communities where it constructed tubes of sand, and in low littoral sand flats. Males taken amongst red algae and sessile epifauna were normally red, but those collected amongst *Cladophoropsis vaucheriaeformis* or from open littoral sand were blue; addition-ally, females within the zosteretum at Amity Point sand bar were also blue. Although this difference in the males was consistent, no other morphological differences were evident. If they were taking on the colour of their surroundings through diet (despite their not being known to be algivorous), then all of the females should also have shown this colouration; if the colour difference were selected for (camouflage), then the two colour morphs must be reproductively isolated, and other distinctions are likely to have co-evolved. The possibility of undistinguished cryptic species cannot be ruled out.

Leptochelia karragarra sp. nov.
(Figs 33–35)

Material Examined. HOLOTYPE: QM-W28138, ♀, sand, north of Banana Bank, Moreton Bay, 27°32.02'S, 153°20.67'E, 4.9 m, 35‰, 28.8°C, 11.02.2005. van Veen grab, RNB. PARATYPES: QM-W28139, ♂ allotype, ♀, dissected, data as for holotype.

Description of Female. Body (Fig. 33A) slender, small, holotype 1.6 mm long, 6.8 times as long as wide. Cephalothorax subrectangular, 1.5 times as long as wide, 1.4 times as long as pereonites 1 and 2 together, with slight rostrum, eyelobes present, eyes black, single setae at posterior of eyelobes and midlaterally. Six free pereonites; pereonites 1 and 2 shortest, pereonites 3 and 6 subequal, slightly longer, pereonites 4 and 5 longest and 1.75 times as long as pereonite 1 (all pereonites respectively 2, 2, 1.5, 1.1, 1.2 and 1.8 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 4.2 times as wide as long, with dorsal setal pair on pereonite 5. Pleotelson (Fig. 33B) semicircular, 2.9 times as wide as long, with two posterolateral setae on each side and two distal setae.

Antennule (Fig. 33D) of four tapering articles, proximal article 2.23 times as long as wide, 1.1 times as long as distal three articles together, with two longer outer and single shorter inner setae; second article 1.25 times as long as wide, distal outer seta 0.58 times as long as article; third article just longer than second with two distal setae and one aesthetasc; fourth article minute, with four distal setae.

Antenna (Fig. 33E) of six articles, proximal article compact, naked; second article as long as
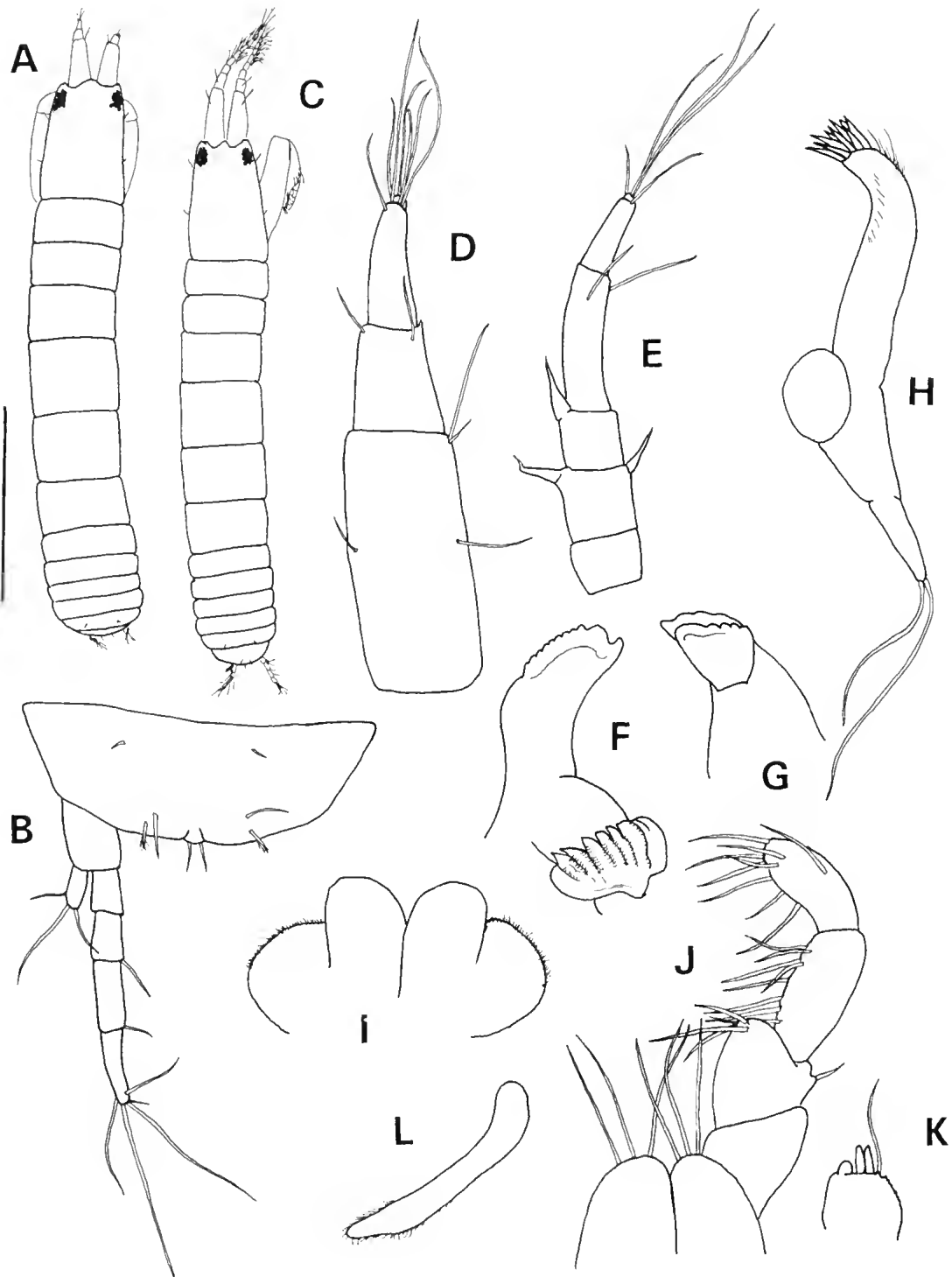
FIG. 33. *Leptochelia karragarra* sp. nov., **A**, holotype female, dorsal; **B**, pleotelson and left uropod; **C**, allotype male, dorsal. **D–L**, paratype female: **D**, antennule; **E**, antenna; **F**, right mandible; **G**, left mandible, distal; **H**, maxillule and maxilla; **I**, labium; **J**, maxilliped; **K**, maxilliped endite; **L**, epignath. Scale bar = 0.5 mm for A, C; 0.1 mm for B, D, E; 0.07 mm for F–L.
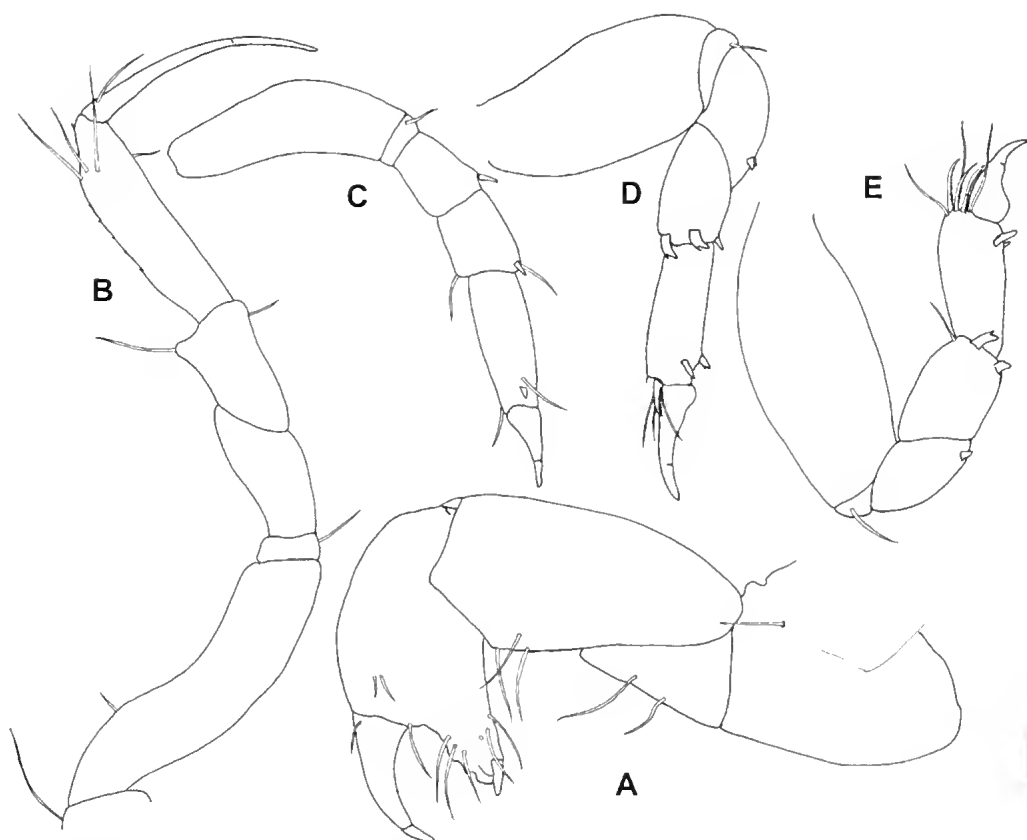
FIG. 34. *Leptochelia karragarra* sp. nov., female paratype, **A**, cheliped; **B** pereopod 1; **C**, pereopod 2; **D**, pereopod 4; **E**, pereopod 6. Scale bar = 0.15 mm for A; 0.1 mm for B–E.

wide, with single inner distal and dorsodistal slender spines; third article as long as wide, with dorsodistal slender spine; fourth article longest, 3.7 times as long as wide, with two distal setae; fifth article 0.6 times as long as fourth; sixth article minute.

Labrum rounded, setose, typical of genus. Right mandible (Fig. 33F) without lacinia mobilis, with crenulation on pars incisiva, pars molaris with strong rugosity; left mandible (Fig. 33G) similar but with crenulate lacinia mobilis wider than distal end of mandible. Labium (Fig. 33I) wide, laterodistally finely setose, without palp. Maxillule (Fig. 33H) with ten distal spines and setose margins, rows of setules sparse on inner distal face; palp distinct, with two distal setae. Maxilliped (Fig. 33J) palp first article naked, second article with one outer and three inner setae, longest inner seta not reaching distal margin of third palp article; third and fourth

articles with filtering rows of six setae and two further inner distal setae, fourth article with outer seta; basis with three long distal setae distal margin of second palp article; endites (Fig. 33K) distally with single seta, one rounded and two robust spatulate spines. Maxilla (Fig. 33H) oval, naked; epignath (Fig. 33L) elongate with setose margin distally.

Cheliped (Fig. 34A) with rounded, compact basis 1.5 times as long as wide; merus sub-triangular with two ventral setae; carpus 2.1 times as long as wide, with three midventral setae; propodus typical for the genus, fixed finger with three ventral and three inner setae, cutting edge crenulate, setal row at base of dactylus of two setae; dactylus with proximal seta.

Pereopod 1 (Fig. 34B) longer than other pereopods, coxa with seta; basis slender, 4.1 times as long as wide; ischium compact with one seta; merus and carpus subequal, merus naked; carpus

with one longer dorsodistal seta one third length of propodus, and one shorter ventrodistal seta; propodus almost as long as carpus and merus together, with four distal setae; dactylus slender, extending into shorter slender unguis, the two together as long as propodus; single proximal seta on dactylus.

Pereopods 2 (Fig. 34C) and 3 similar to each other, more compact than pereopod 1, basis 3.1 times as long as wide; ischium with 1 seta; merus as long as carpus, merus with strong ventrodistal spine, carpus with ventrodistal spine and adjacent seta, and dorsodistal seta; propodus 1.8 times as long as carpus, with ventrodistal spine and adjacent seta, and dorsodistal seta; dactylus and short unguis together 0.6 times as long as propodus.

Pereopods 4 (Fig. 34D) and 5 similar to each other, basis stout, 1.8 times as long as wide; ischium with one seta; merus shorter than carpus, merus with two short, ventrodistal spines, carpus with outer, ventral and inner distal spines each with fine outer setule; propodus 1.4 times as long as carpus, with two distal slender spines, three distal setae half as long as dactylus plus unguis, and distal serrated spine; dactylus and unguis partially fused into a claw, curved, 0.8 times as long as propodus.

Pereopod 6 (Fig. 34E) similar to pereopod 4, but propodus more compact, without distal serrated spine but with three pectinate and three simple distal setae.

Pleopods all alike, typical for the genus, with naked basis.

Uropod (Fig. 33B) biramous, basis naked; exopod of one segment, as long as proximal endopod segment, with median outer seta and with outer distal seta longer than inner distal seta; endopod of four segments, distal segments slender.

Description of Male. Just smaller than female (allotype length 1.4 mm), body (Fig. 33C) of similar proportion, cephalon as long as pereonites 1–3 together. Sexual dimorphism as follows.

Antennule (Fig. 35A) elongate, first peduncle article 4 times as long as wide with single distal seta; second article half as long as first with single outer-distal seta and three ventrodistal setae; third article 0.6 times as long as second, with single dorsodistal seta; flagellum of 7 seg-

ments, distal two minute; proximal flagellum segment with tufts of 7 proximal and 6 distal aesthetascs, subsequent segments each bearing distal tufts of 6, 6, 5, 5, 4 and 0 aesthetascs respectively. Antenna (Fig. 35B) more slender than that of female, articles 4 and 5 subequal in length. Mouthparts atrophied.

Cheliped (Fig. 35C) more slender than that of female; carpus 3 times as long as wide, with small ventrodistal invagination to accommodate propodus on reflexion; propodus with setal row at base of dactylus of 12 setae, fixed finger shorter than palm, with single inner tooth-like apophyses on cutting edge; moveable finger with stout setae along cutting edge.

Pereopod 1 (Fig. 35D) carpus with longest distal seta as long as carpus; dactylus plus unguis shorter than propodus. Spines on merus and carpus of pereopods 2–6 (e.g. Figs 32E, F) longer and more slender than those of female, pereopods 4 (Fig. 35F) and 5 without distal serrated spine on propodus.

Etymology. *Karragarra* is the Goenpul Aboriginal name for an island in the south of Moreton Bay.

Remarks. All of the three previously described species of *Leptochelia* with only three distal maxilliped basis setae (*L. nobbi*, *L. itoi* and *L. lusei*) have their uropod exopod much shorter than the proximal endopod article, whereas in *L. karragarra* sp. nov. these articles are equal in length. In most respects (other than number of maxilliped basis setae), the present species is closest to *L. daggi* from southwest Australia, but differs in having the longest distal seta on antennule peduncle article 2 much shorter than article length (1.4 times as long in *L. daggi*), the dactylus plus claw on pereopod 1 as long as propodus (1.25 times as long in *L. daggi*), and the cheliped basis 1.5 times as long as wide (only as long as wide in *L. daggi*). The antennule peduncle basal article, at 2.23 times as long as wide, is much more compact in *L. karragarra* than in all of the species mentioned above (at least 2.5 times as long as wide. The male is typical of a primary male for the genus, but with a shorter chela with only a single tooth-like apophysis on the fixed finger (perhaps related to its small size), and no elaborations on the cheliped carpus or pereopod 6 basis. *L. karragarra* is the smallest species of the genus yet described.
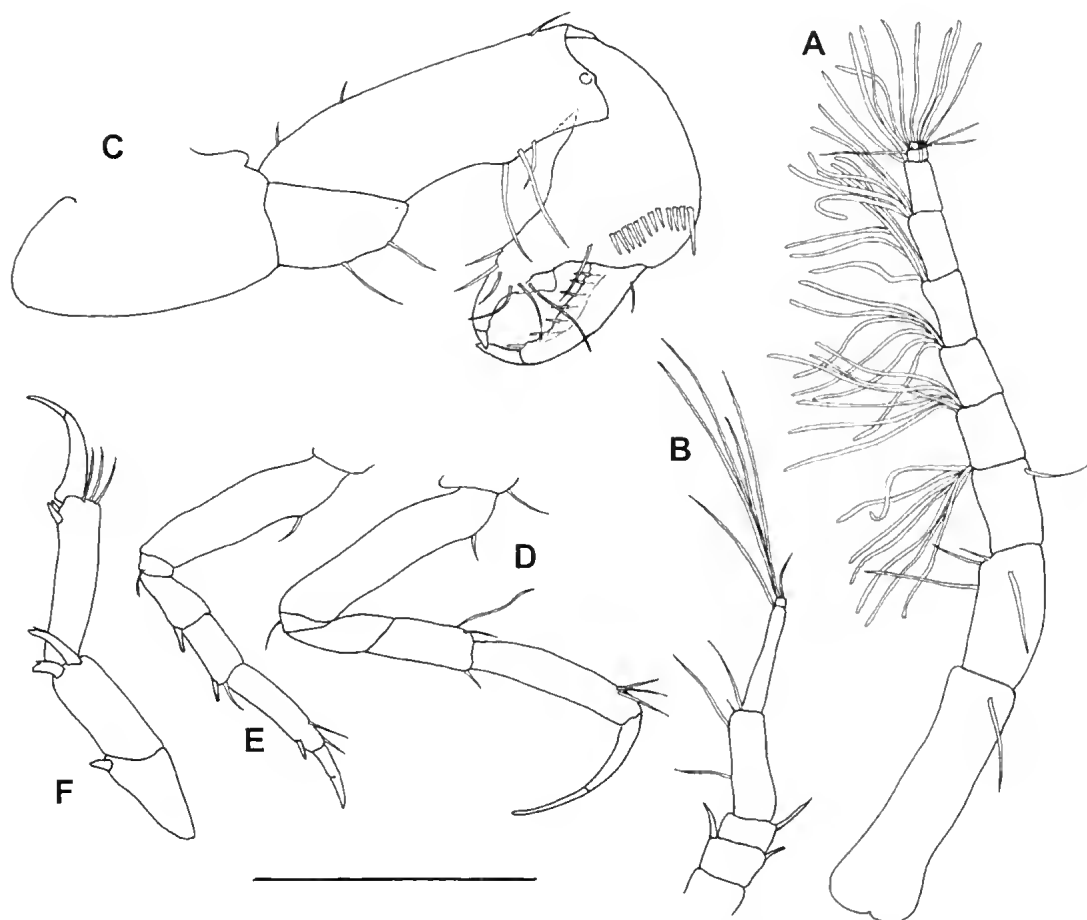
FIG. 35. *Leptochelia karragarra* sp. nov., allotype male, **A**, antennule; **B**, antenna; **C**, cheliped; **D**, pereopod 1; **E**, pereopod 3; **F**, distal articles of pereopod 4. Scale bar = 0.2 mm for A–E; 0.15 mm for F.

The present species occurred towards the southern end of Moreton Bay, sublittorally in sedimentary infauna in clean sand, probably interstitially.

Leptochelia guduroo sp. nov.
(Figs 36, 37)

Material Examined. HOLOTYPE: QM-W28140, ♀, medium sand with coarse shell breccia and ophiuroids, southeast of Bribie I., northwest of Moreton Bay, 27°03.17'S, 153°13.17'E, 10.2 m, 35‰, 28.5 °C, 22.02.2005, long-arm van Veen grab, RNB. PARATYPES: QM-W28141, ♀, 3 juvs, NHM 2006.1649, ♀ with oostegites, dissected, data as for holotype.

Description. Female body (Fig. 36A) slender, holotype 4 mm long, 7.2 times as long as wide. Cephalothorax subrectangular, 1.35 times as long as wide, as long as pereonites 1 and 2 together,

with slight rostrum, eyelobes and black eyes present, single setae midlaterally. Six free pereonites; pereonite 1 shortest, pereonites 2, 3 and 5 subequal, pereonite 6 slightly shorter, pereonite 4 longest and 1.7 times as long as pereonite 1 (all pereonites respectively 1.9, 1.4, 1.3, 1.1, 1.4 and 1.7 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 4.5 times as wide as long, naked. Pleotelson (Fig. 36B) semicircular, shorter than last two pleonites together, nearly three times as wide as long, with single posterolateral setae on each side and two distal setae.

Antennule (Fig. 36C) of four tapering articles, proximal article 2.8 times as long as wide, 1.3 times as long as distal three articles together, with two long outer distal and inner and ventral setae at midlength; second article 1.5 times as
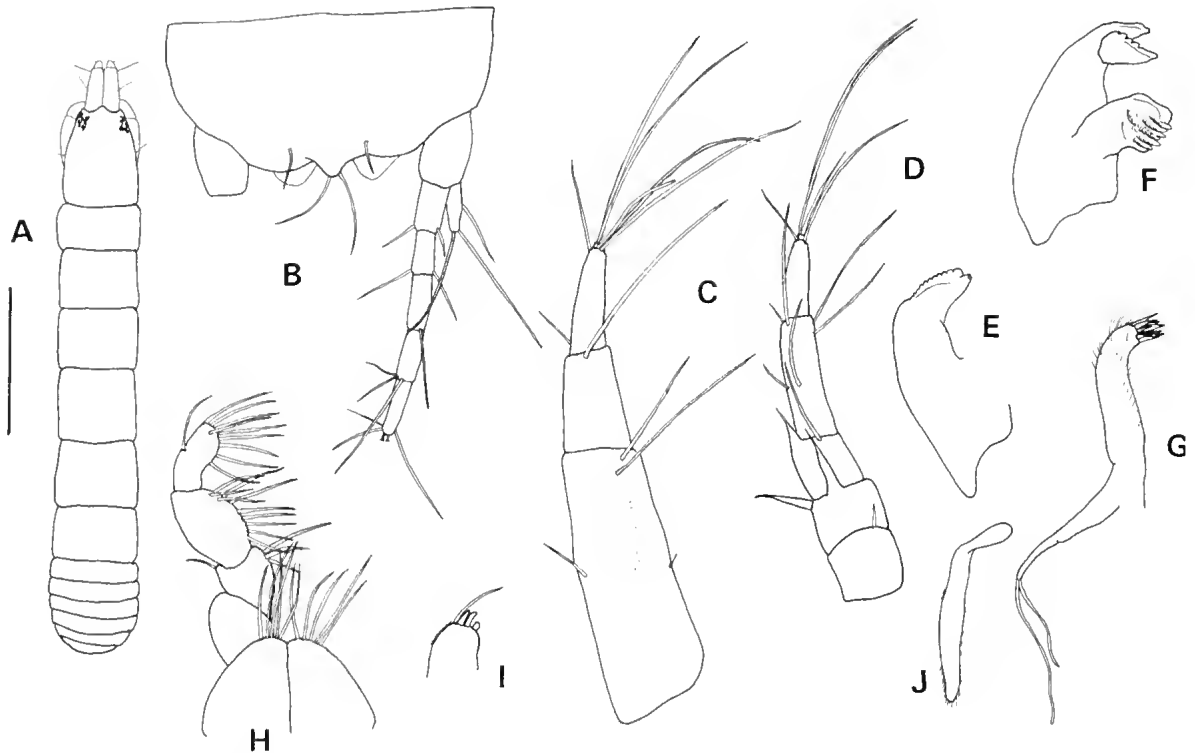
FIG. 36. *Leptochelia guduroo* sp. nov., **A**, holotype female, dorsal; **B**, pleotelson and right uropod; **C**, antennule; **D**, antenna; **E**, right mandible (pars molaris detached); **F**, left mandible; **G**, maxillule; **H**, maxilliped; **I**, maxilliped endite; **J**, epignath. Scale bar = 1 mm for A; 0.2 mm for B–J.

long as wide, distal outer seta twice as long as article; third article as long as second, with three distal setae and one aesthetasc; fourth article minute, with two distal setae.

Antenna (Fig. 36D) of six articles, proximal article compact, as long as wide, with single distal seta; second article shorter than first, with single outer distal and dorsodistal slender spines; third article as long as wide, with dorsodistal slender spine and outer seta longer than article; fourth article longest, 3.5 times as long as wide and twice as long as third article, with median and distal setae longer than fifth article; fifth article 0.65 times as long as fourth; sixth article minute.

Labrum rounded, setose, typical of genus. Left mandible (Fig. 36F) with crenulate lacinia mobilis not wider than distal end of mandible, slight crenulation on pars incisiva, pars molaris with strong rugosity; right mandible (Fig. 36E) similar but without lacinia mobilis. Labium (not figured)

wide, distally finely setose, without palp. Maxillule (Fig. 36G) with ten distal spines and setose dorsal margin, rows of setules on inner face towards ventral margin; palp distinct, with two distal setae. Maxilliped (Fig. 36H) palp first article naked, second article with one outer and three inner setae, distal-most inner seta shorter than third palp article; third and fourth articles each with filtering rows of eight setae, third article with two further inner distal setae, fourth article with outer seta and submarginal inner distal seta; basis with five long setae extending to distal margin of second palp article; endites (Fig. 36I) distally with single seta, one inner rounded and two robust spatulate spines. Maxilla (not figured) oval, naked; epignath (Fig. 36J) elongate with setose margin distally.

Cheliped (Fig. 37A) with rounded, compact basis 1.4 times as long as wide; merus subtriangular with two shorter and one longer ventral setae; carpus 1.8 times as long as wide, with
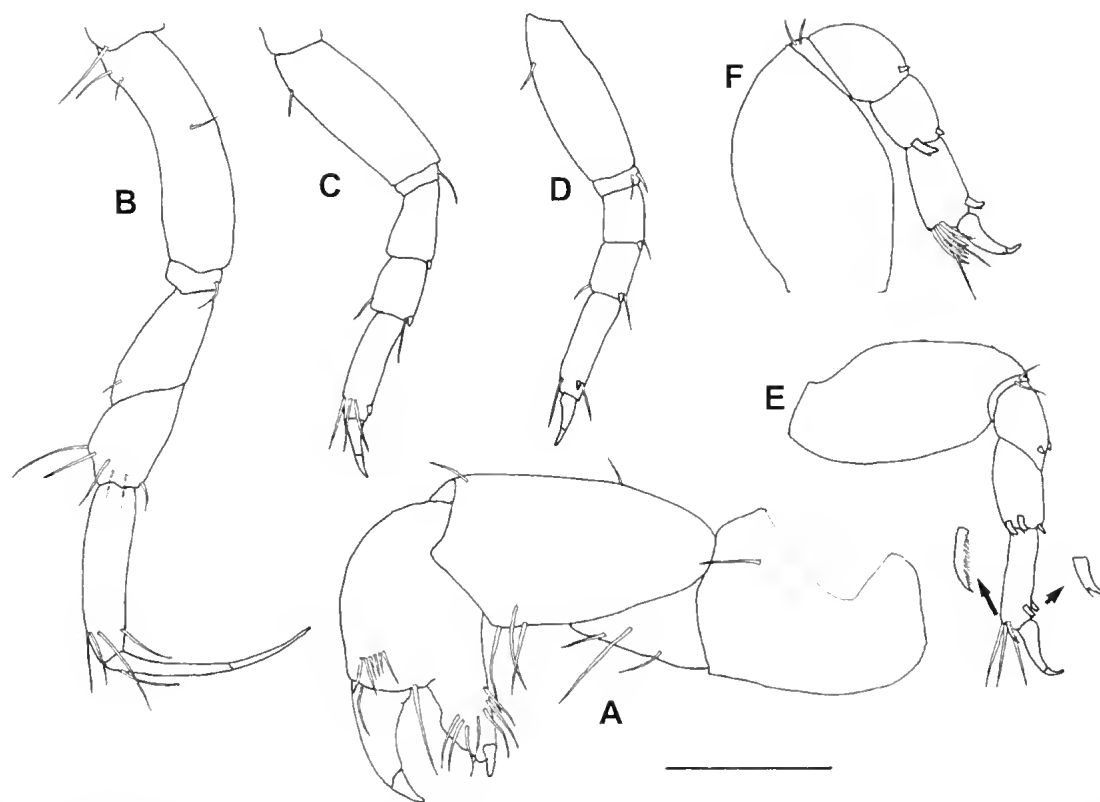
FIG. 37. *Leptochelia guduroo* sp. nov., **A**, cheliped; **B–E**, pereopods 1–4 respectively; **F**, pereopod 6. Scale bar = 0.15 mm for A; 0.2 mm for B–F.

three ventrodistal setae; propodus typical for the genus, fixed finger with three ventral and four inner setae, cutting edge raised distally; setal row at base of dactylus of six setae; dactylus with proximal seta.

Pereopod 1 (Fig. 37B) longer than other pereopods, coxa with seta; basis 3.8 times as long as wide; ischium compact, naked; merus just longer than carpus, with single dorsodistal seta; carpus with one ventrodistal, two inner distal and three dorsodistal setae, longest of which is half length of propodus; propodus 0.9 times as long as carpus and merus together, with four distal setae; dactylus slender, extending into shorter slender unguis, the two together 1.14 times as long as propodus; single proximal seta on dactylus. Pereopod 2 (Fig. 37C) more compact than pereopod 1; ischium with one seta; merus 1.25 times as long as carpus, merus with small ventrodistal spine, carpus with ventrodistal spine and adjacent seta and dorsodistal seta; propodus nearly twice as long as carpus, with three dorso-distal setae and single ventrodistal spine; dactylus and short unguis together 0.55 times as long as propodus. Pereopod 3 (Fig. 37D) similar to pereopod 2, but ischium with two setae, carpus and merus of equal length, and propodus with two distal setae.

Pereopod 4 (Fig. 37E) basis stout, 1.6 times as long as wide; ischium with two setae; merus shorter than carpus, with two short, ventrodistal spines, carpus with outer, ventral and inner distal spines each with fine outer setule; propodus 1.2 times as long as carpus, with two ventrodistal stout spines with fine outer setule and one mid-distal pectinate spine, three distal setae as long as dactylus plus unguis; dactylus and unguis partially fused into a claw, curved. Pereopod 5 as pereopod 4. Pereopod 6 (Fig. 37F) as pereopod 4, but single distal carpal spine larger, propodus with five pectinate and two simple distal setae, and no mid-distal spine.

Pleopods all alike, typical for the genus, with single dorsal plumose seta on basis.

Uropod (Fig. 36B) biramous, basis naked; exopod of one segment as long as proximal endopod segment, with mid-outer short seta and outer distal seta longer than inner distal seta; endopod of five segments, distal segments slender.

Male unknown.

Etymology. After *Nguduroo*, a local Aboriginal name for an island in the south of Moreton Bay.

Remarks. *Leptochelia guduroo* sp. nov. is distinguished from all other described species of *Leptochelia* by the long setae on the antenna and antennule; the longest distal seta on article two of the antennule peduncle is twice as long as the article itself, while the distal setae on peduncle article four of the antenna are longer than article five. Of the other taxa with five distal setae on the maxilliped basis, only *L. dijonesae* and *L. savignyi sensu* Shiino, 1965 have the carpus of pereopod two shorter than the merus; the former species is distinguished by having a two segmented uropod exopod (see above), while the latter has a more slender cheliped, a uropod exopod shorter than the first endopod segment, the dactylus plus unguis of pereopod 1 shorter than the propodus, and the longest distal seta on the antennule article two less than the length of the article. Neither of these species (nor any other) has the long distal seta on antenna article three or at midlength on antenna article four.

Leptochelia guduroo was only found in sublittoral coarse sand at 10.2 m depth at the northwest corner of Moreton Bay.

Pseudoleptochelia Lang, 1973

Pseudoleptochelia fairgo Bamber, 2005

Pseudoleptochelia fairgo Bamber, 2005: 699–705, figs 44–46.

Material Examined. QM-W28142, 219 ♀♀ (5 brooding), coarse sand and shell with *Branchiostoma*, Moreton Bay, 27°27.0'S, 153°18.8'E, 8.4–9.9 m, 35‰, 29.4°C, 10.02.2005, spanner-crab dredge. QM-W28143, 7 ♀♀ (1 brooding), amongst *Halophila decipiens* on slightly anoxic sand, NE of Chain Banks, Moreton Bay, 27°24.59'S, 153°21.68'E, 7.7 m, 35‰, 29.4°C, 10.02.2005, van Veen grab. QM-W28144, 2 ♀♀ with oostegites, amongst *Halophila decipiens* on slightly anoxic sand, NE of Chain Banks, Moreton Bay, 27°24.58'S, 153°21.75'E, 7.7–8.5 m, 35‰, 28.8°C, 11.02.2005, spanner-crab dredge. 1 damaged ♀ without oostegites, amongst *Halophila decipiens* on sand with some shell, west side

of Moreton I., Moreton Bay, 27°16.90'S, 153°23.20'E, 4.7 m, 35‰, 28.6°C, 10.02.2005, van Veen grab. QM-W28145, 32 ♀♀ (2 brooding) muddy sand with fine shell breccia, Moreton Bay, 27°28.66'S, 153°21.34'E, 7.2 m, 35‰, 29°C, 1.02.2005; van Veen grab. NHM 2006.1650–1651, 2 ♀♀ (in ethanol), sand, north of Banana Bank, Moreton Bay, 27°32.02'S, 153°20.67'E, 4.9m, 35‰, 28.8°C, 11.02.2005; van Veen grab. QM-W28146, 2 ♀♀ (1 brooding), medium muddy sand with shell, NE of Banana Bank, Moreton Bay, 27°32.53'S, 153°20.99'E, 4.2 m, 35‰, 28.8°C, 11.02.2005; van Veen grab. QM-W28147, 2 ♀♀, sandy mud with seagrass, Banana Bank, Moreton Bay, 27°32.46'S, 153°20.74'E, 3.1 m, 33‰, 28°C, 17.02.2005, van Veen grab, all RNB. QM-W28451, 6 ♀♀, MBWS Stn. 10; van Veen grab, PJFD.

Remarks. *Pseudoleptochelia fairgo* was previously known from the type collection at Esperance Bay, southwestern Australia, where it was the commonest tanaidomorph, living in sandy substrata at depths between 23–40 m. The present material is from similar substrata, although from shallower depths (3–10 m). The antennule of this species is relatively compact (although less so than that of *Konarus cheiris*), the dactylus plus unguis on the first pereopod is longer than the propodus, and the uropod exopod is much longer than the proximal endopod article, with incipient separation into two segments. It is recognisable from other Australian leptocheliids by the lack of strong spines on the antenna, the group of elongate distal setae on the cheliped merus (the longest as long as the merus, and pointing proximally in life) and its unique possession of setose tubercles on pereopods 4–6.

Pseudoleptochelia straddi sp. nov.
(Fig. 38)

Material Examined. HOLOTYPE: QM-W28148, ♂ amongst empty *Phoronis* tubes, Point Lookout, North Stradbroke I., 27°26.31'S, 153°32.52'E, 10 m, 12.02.2005, A-NL.

Description. Male body (Fig. 38A) compact, holotype 2.6 mm long, 4.5 times as long as wide. Cephalothorax subpentangular, 1.3 times as long as wide, as long as first four pereonites together, with pronounced rostrum, large eyelobes and eyes present, eyes black. Six free pereonites; pereonite 1 shortest, pereonites 2, 3 and 6 subequal, pereonites 4 and 5 subequal, longest and nearly twice as long as pereonite 1 (all pereonites respectively 4.8, 4.0, 3.8, 2.4, 2.3 and 3.1 times as wide as long). Pleon of five free sub-
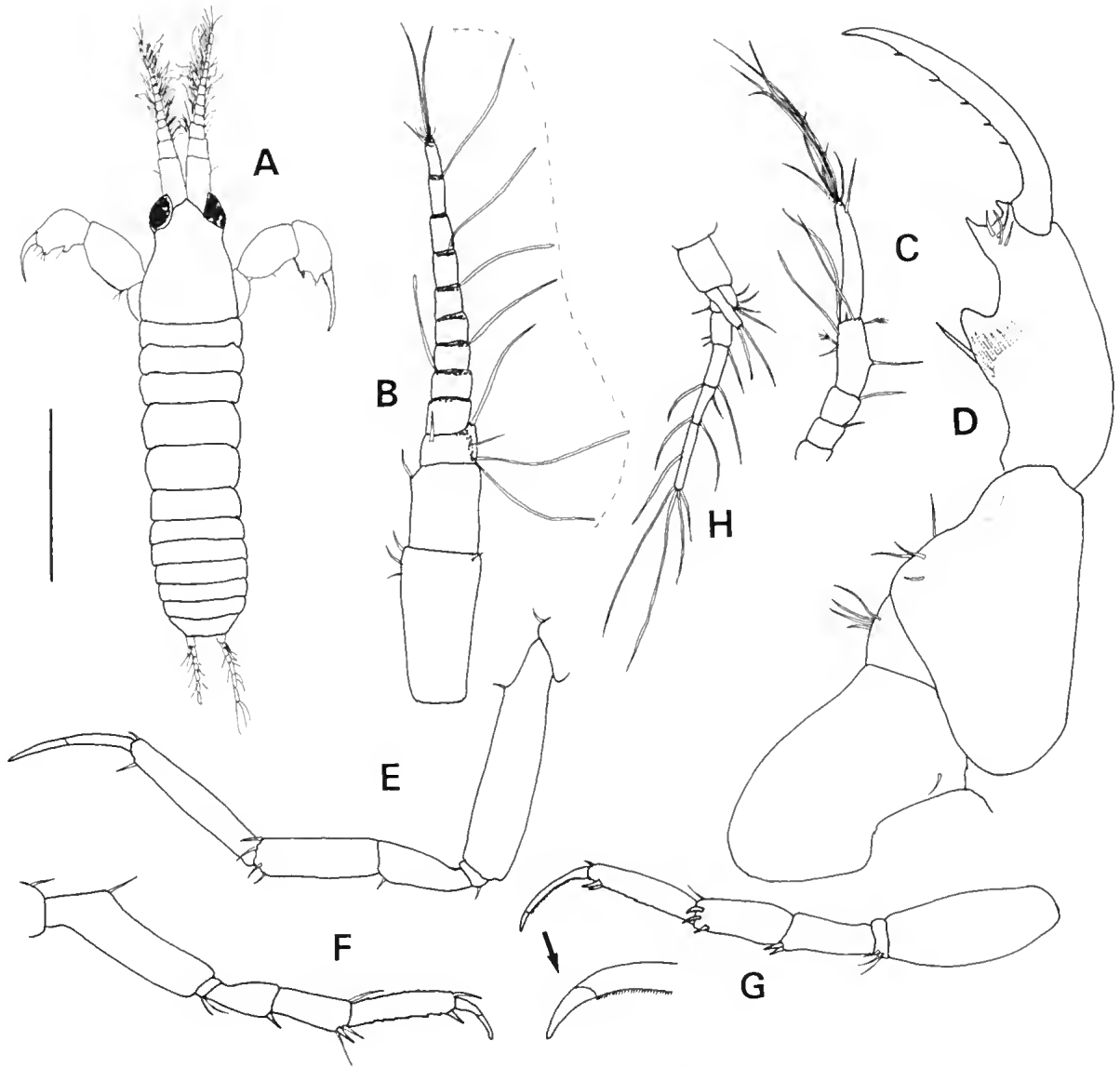
FIG. 38. *Pseudoleptochelia straddi* sp. nov., holotype male: **A**, holotype, dorsal; **B**, antennule; **C**, antenna; **D**, cheliped; **E**, pereopod 1; **F**, pereopod 3; **G**, pereopod 5; **H**, uropod. Scale bar = 1 mm for A; 0.3 mm for B–H.

equal pleonites bearing pleopods; each pleonite about 4.5 times as wide as long. Pleotelson trapezioid, as long as last pleonite, 4 times as wide as long, with two posterodistal setae on each side and two mid-distal setae.

Antennule (Fig. 38B) peduncle of three articles, proximal article twice as long as wide, with three short outer distal setae; second article 0.6 times as long as first; third article one-third length of second, with inner distal seta 4 times as long as article. Flagellum of 11 articles; first

segment hidden beneath distal peduncle article, segments 2–6 wider than long, segments 7–10 longer than wide, distal segment minute and bearing 4 short curved and two long distal setae. Segments 1–10 bearing 18, 16, 15, 14, 13, 13, 10, 6, 5 and 5 distal aesthetascs respectively.

Antenna (Fig. 38C) of six articles, proximal article compact, naked; second and third articles with single dorsodistal setae; fourth article as long as first three together, twice as long as wide, with single mid-dorsal seta longer than

article width, three distal setae longer than article length, small mid-ventral seta, and two sensory setae; fifth article longest, 1.5 times as long as fourth; sixth article minute.

Mouthparts atrophied.

Cheliped (Fig. 38D) subchelate, with rounded, compact basis 1.6 times as long as wide; merus subtriangular with four ventral setae; carpus with curved proximal expansion overlapping basis, 1.7 times as long as wide, with four mid-ventral setae; propodus with mid-ventral rounded apophysis and adjacent setal row, ventrodistal apophysis ('fixed finger') pointed and with four short setae; dactylus just longer than propodus, with short, stout setae along cutting edge.

Pereopod 1 (Fig. 38E) longer than other pereopods, coxa with seta; basis slender, 4.2 times as long as wide; ischium compact with one seta; merus half length of basis, with single short ventrodistal seta; carpus 1.3 times as long as merus, with 4 short distal setae; propodus 1.3 times as long as carpus; dactylus slender, extending into subequal slender unguis, the two together 0.8 times as long as propodus. Pereopods 2 and 3 (Fig. 38F) similar to each other, more compact than pereopod 1; basis 3.7 times as long as wide; ischium with 2 setae; merus 0.8 times as long as carpus, with slender ventrodistal spine; carpus with slender ventrodistal spine and two ventrodistal and single dorsodistal setae; propodus with slender ventrodistal spine and dorsodistal seta; dactylus and unguis curved, together half as long as propodus.

Pereopods 4, 5 (Fig. 38G) and 6 similar to each other; basis stouter than on anterior pereopods, 2.5 times as long as wide; ischium with three setae; merus with two slender ventrodistal spines; carpus just longer than merus, with outer, ventral and inner distal spines; propodus longer than carpus, with two ventrodistal slender simple spines; dactylus and short unguis slender, curved, dactylus finely serrate along ventral margin.

Pleopods all alike, typical for the genus, with single dorsal plumose seta on basis.

Uropod (Fig. 38H) biramous, basis naked; exopod of one segment, 1.8 times as long as proximal endopod segment, with outer mid-length seta and two distal setae, outer distal seta longer than inner distal seta; endopod of five, pro-

gressively longer segments, with distal segments slender.

Etymology. 'Straddy' is the colloquial name for North Stradbroke Island.

Remarks. The only other species of *Pseudoleptochelia* described from Australia is *P. fairgo* (see above). The large number of female *Pseudoleptochelia* collected from Moreton Bay showed a morphology not significantly distinguishable from that south-western-Australian species, although there are slightly more setae on the cheliped merus. The male of *P. fairgo* is immediately distinct from the present species in its cheliped morphology, *P. fairgo* being without the mid-ventral, rounded apophysis on the propodus present in *P. straddi* sp. nov., and having a carpus expanded into a rounded apophysis mid-ventrally, rather than extended proximodorsally as in *P. straddi*. Antennal and pereopod morphology of the two is similar.

If the Moreton Bay *P. fairgo* material represents a sibling species distinguishable only by the males, this can only be resolved by molecular analysis. However, no females of this genus were collected in the epizoic habitats at Point Lookout in which the present male was taken; rather, *P. fairgo* is a denizen of open soft-sediment habitats.

Catenarius gen. nov.

Diagnosis. Typical tanaidomorph of the Leptocheliidae, dorsoventrally flattened; cephalon with a slight, rounded rostrum, eyelobes and pigmented eyes; antennule of five articles in the female, articles two to four subequal in length; antenna of six articles with dorsal and ventral distal spines on article 2 and dorsodistal spine on article 3. Mandibles, maxillule, labrum, labium typical of *Leptochelia*. Maxilliped basis with three distal setae; endite with two distal pointed spines, inner distal square apophysis, outer distal setulose seta. Cheliped slender. Pereopods generally typical of *Leptochelia*: pereopod 1 dactylus and unguis together longer than propodus; pereopods 2 and 3 with small ventrodistal spine; pereopods 4–6 with sparse setation and simple spines. Five free pleonites without plumose lateral setae, all bearing biramous pleopods, pleopod basis naked. Uropods biramous, exopod of two segments, endopod of five segments.

Type Species: *Catenarius daviei* sp. nov., by original designation.

Etymology. *Catenarius* is from the Latin 'of a chain', referring to Chain Banks, the type locality.

Remarks. The new genus is distinguished from the majority of species described in *Leptochelia* by its five-articled antennule in the female, and from all of them by the sharp distal spines on the maxilliped endite. Three other species attributed to *Leptochelia* exhibit a five-articled antennule (presuming that they have a minute distal article), viz. *Leptochelia saviguyi sensu* Sars, 1886, from the Mediterranean (Italy), *Leptochelia elongata* Larsen & Rayment, 2002, from the Andaman Sea (Thailand), and *Leptochelia saviguyi* (Krøyer, 1842) *sensu stricto*, which Smith (1906) considered to represent an immature male stage (the present specimen is a mature female). All of these species have a one-segmented uropod exopod. The only one of these species for which the maxilliped endite ornamentation is known is *L. elongata*, and that species has a 'normal' distal set of two spatulate and one rounded spines. If these two features of uropod exopod and maxilliped endite spination are diagnostic of the new genus, then it remains difficult to attribute these other species thereto. Conversely, it may be useful to separate those taxa with five-articled antennules from the remaining species of *Leptochelia*.

Catenarius daviei sp. nov.
(Figs 39, 40)

Material Examined. HOLOTYPE: QM-W28149, ♀ with empty brood pouch, amongst *Halophila decipiens* on slightly anoxic sand, NE of Chain Banks, Moreton Bay, 27°24.59'S, 153°21.68'E, 7.7 m, 35‰, 29.4°C, 10.02.2005, van Veen grab, RNB.

Description. Female body (Fig. 39A) slender, holotype 2.75 mm long, 6.5 times as long as wide. Cephalothorax subrectangular, just longer than wide, shorter than pereonites 1 and 2 together, with slight rostrum, eyelobes and black eyes present. Six free pereonites, pleonites 1–3 with single anterolateral setae; pereonite 1 shortest, pereonites 2, 3 and 5 subequal, pereonite 6 shorter, pereonite 4 longest and twice as long as pereonite 1 (all pereonites respectively 2.13, 1.4, 1.4, 1.1, 1.4 and 1.6 times as wide as long). Pleon of five free subequal pleonites bearing pleopods; each pleonite about 5 times as wide as long,

with single midlateral setae. Pleotelson semicircular, as long as last two pleonites together, twice as wide as long, with two posterolateral setae on each side and two distal setae.

Antennule (Fig. 39B) of five tapering articles, proximal article 3 times as long as wide, 1.3 times as long as distal four articles together, with two long outer and single long dorsal setae; second article 1.5 times as long as wide, 0.3 times as long as proximal article, distal outer seta shorter than article; third and fourth articles subequal, just shorter than second, fourth article with three distal setae and single aesthetasc; fifth article minute, eccentric, with two distal setae.

Antenna (Fig. 39C) of six articles, proximal article compact, with distal seta; second article longer than wide, with ventrodistal and dorsodistal slender spines; third article longer than wide, as long as second article, with dorsodistal slender spine; fourth article 1.6 times as long as third, 3.6 times as long as wide; fifth article just longer than fourth; sixth article minute.

Labrum (Fig. 39E) rounded, setose. Left mandible (Fig. 39F) with crenulate lacinia mobilis narrower than distal end of mandible, proximal crenulation on pars incisiva, pars molaris with strong rugosity; right mandible similar but without lacinia mobilis. Labium (not figured) wide, distally finely setose, without palp. Maxillule (Fig. 39D) with ten distal spines and setose margins, rows of setules on inner distal face; palp distinct, with two distal setae. Maxilla not seen. Maxilliped (Fig. 39G) palp first article naked, second article with one outer and three inner setae, distal-most inner seta almost reaching distal margin of third palp article; third and fourth articles with filtering rows of six and five setae respectively, third article with two further inner distal setae, fourth article with two mesial setae; basis with three long setae extending to third palp article; endites (Fig. 39H) distally with single outer setulose seta, two pointed spines and slight inner square apophysis. Epignath not seen.

Cheliped (Fig. 40A) with rounded, slender basis 1.5 times as long as wide; merus subtriangular with one longer and one small ventral setae; carpus 2.3 times as long as wide, with three ventrodistal setae, sparse small dorsal setae;
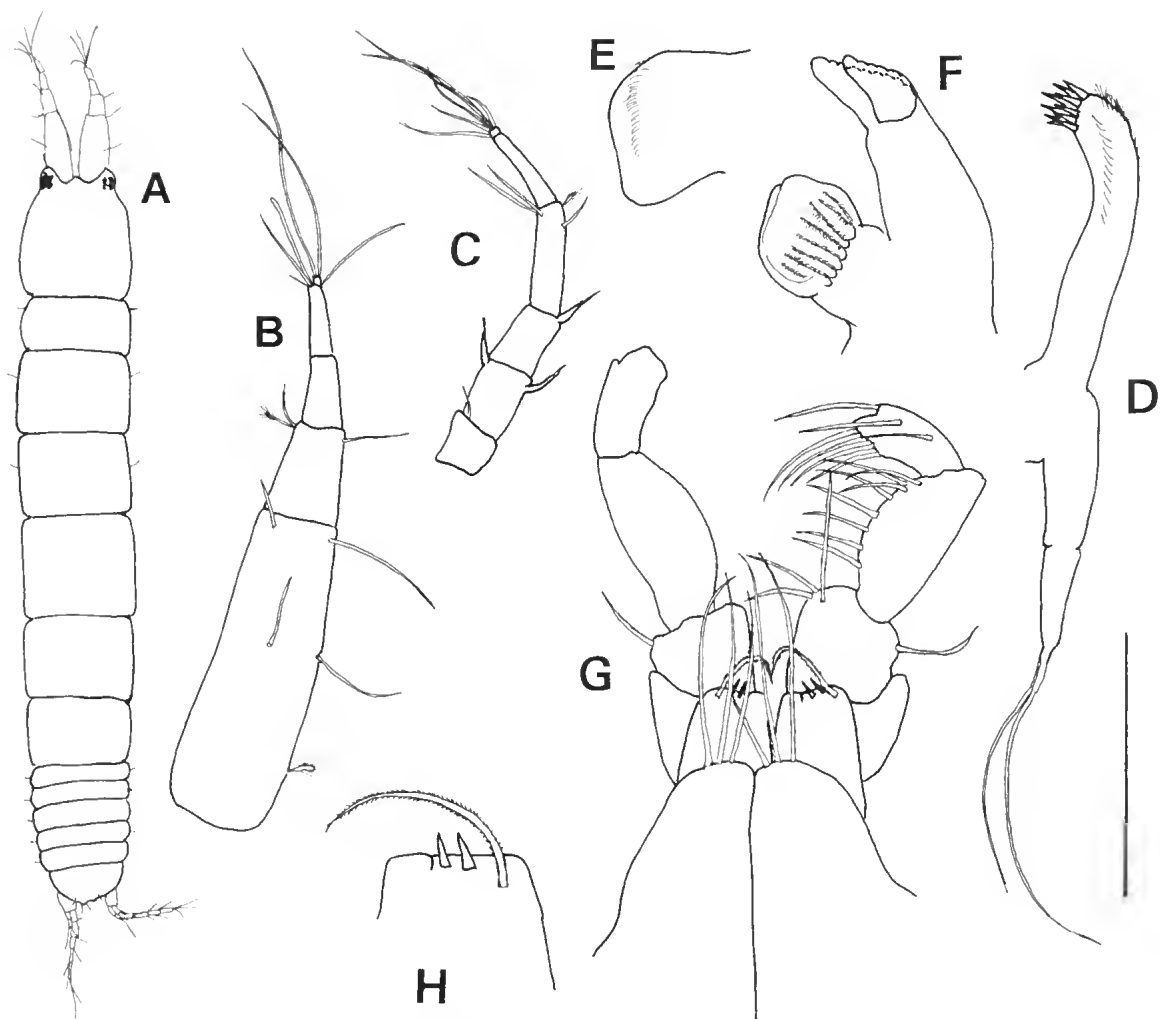
FIG. 39. *Catenarius daviei* gen. et sp. nov., female holotype, A, body, dorsal; B, antennule; C, antenna; D, maxillule; E, labrum, lateral; F, left mandible; G, maxilliped (inner setae of right palp not shown); H, detail of maxilliped endite. Scale bar = 1 mm for A; 0.2 mm for B, C; 0.1 mm for D–H.

propodus palm longer than fingers of chela, fixed finger with two ventral and three inner setae, cutting edge hardly crenulate, setal row at base of dactylus of two setae; dactylus with proximal seta.

Pereopod 1 (Fig. 40B) longer than other pereopods, coxa with seta; basis slender, 3.6 times as long as wide, with proximal seta; ischium compact with one ventral seta; merus axially as long as carpus, naked; carpus with long dorsodistal seta 0.4 times length of propodus; propodus as long as carpus and merus together, with three dorsal and one ventral distal setae; dactylus slender, extending into shorter slender unguis, the two

together some 1.2 times as long as propodus; single proximal seta on dactylus. Pereopod 2 (Fig. 40C) more compact than pereopod 1; basis 2.7 times as long as wide, ischium with 2 setae; merus as long as carpus, merus with small dorsodistal spine, carpus with short ventrodistal spine and adjacent seta, single dorsodistal seta; propodus 1.5 times as long as carpus, with short ventrodistal spine and two dorsodistal setae; dactylus and unguis together 0.6 times as long as propodus. Pereopod 3 similar to pereopod 2.

Pereopods 4 and 5 (Fig. 40D) similar to each other, basis stout, twice as long as wide; ischium with two setae; merus 0.6 times as long
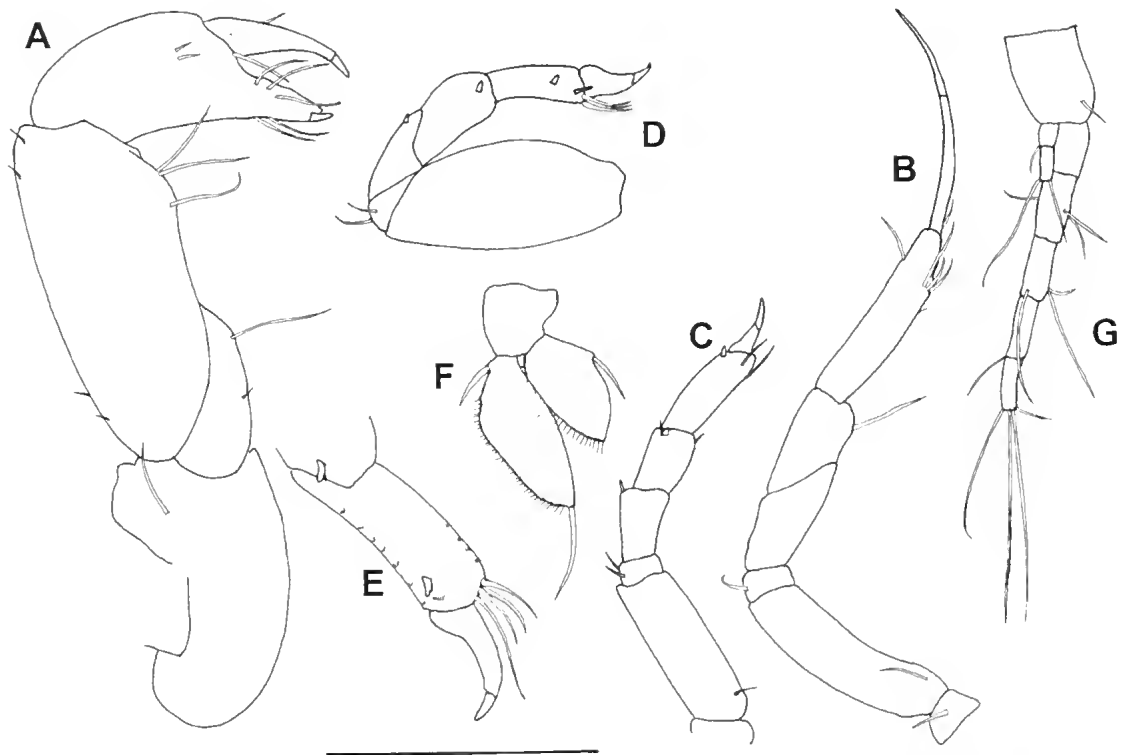
FIG. 40. *Catenarius daviei* gen. et sp. nov., female holotype, **A**, cheliped; **B**, pereopod 1; **C**, pereopod 2; **D**, pereopod 5; **E**, distal articles of pereopod 6; **F**, pleopod; **G**, uropod. Scale bar = 0.2 mm for A–D, F, G; 0.1 mm for E.

as carpus, with two short, ventrodistal spines, carpus with single outer and inner simple distal spines; propodus as long as carpus, with one subdistal and one distal simple spines, three dorsodistal setae more than half as long as dactylus plus unguis; dactylus and unguis partially fused into a claw, curved. Pereopod 6 (Fig. 40E) as pereopod 5, but propodus with single subdistal spine and three shorter and one longer simple distal setae.

Pleopods (Fig. 40F) all alike, with naked basis.

Uropod (Fig. 40G) biramous, basis with inner distal seta; exopod of two segments, 1.1 times as long as proximal endopod segment, outer distal seta longer than inner distal seta; endopod of five segments, distal segments slender.

Male unknown.

Etymology. In gratitude to Peter Davie for his organisation of the 2005 Moreton Bay Workshop and his assistance with this paper.

Remarks. The five-articled antennule is rare amongst the Leptocheliidae, and the pointed distal spines on the maxilliped endite unique (see above under generic remarks), on which basis the species is placed in a new genus. In comparison with *Leptochelia* species, only *L. dijonesae* has a two-segmented uropod exopod, but that species has four or five maxilliped basis setae. All of the three species with three distal maxilliped basis setae (*L. itoi*, *L. lusei* Bamber & Bird 1997, and *L. nobbi*) have single-segmented uropod exopods shorter than the proximal uropod endopod segment, and have a proportionately shorter cheliped carpus, a proportionately longer cheliped basis, a proportionately shorter merus and longer propodus on pereopods 2 and 3, and generally more substantial spines and setation on the pereopods.

DISCUSSION

The directed collecting in Moreton Bay has confirmed the unusually high diversity of tanaidaceans in Australian inshore waters, as found in Western Australia by Bamber (2005), and more locally by Larsen (2001) in New South Wales

within *Paratanais*. These results indicate that the Australian tanaidacean fauna is severely under-recorded. That will, in part, account for the fact that, of the thirty species recorded herein, only six are known from elsewhere in Australia, one from Victoria (*Remexudes toompani*), two from New South Wales (*Bathytanais bathybrotes, B. juergeni*), two from Western Australia (*B. culteriformis, Pseudoleptochelia fairgo*) and one from Northern Territory (*Gollumudes larakia*). One other, *Konarus cheiris*, is known from the other side of the Coral Sea in New Caledonia.

Equally, there is increasing evidence that species of tanaidacean are not normally widespread, hardly surprising for taxa with no active dispersal phase in their life-history. Rather, they demonstrate localised diversity via niche specificity, as was found in 'sympatric' *Leptochelia* species in Hong Kong by Bird & Bamber (2000).

The habitat specificity of apparently sympatric *Bathytanais* species in Moreton Bay is discussed above. Equally, the two species of *Pakistanapseudes* which were collected more than once showed different habitat preferences, *P. australianus* occurring in muddy sands in the middle of Moreton Bay (Middle Banks of Guţu 2006), while *P. perulpa* was taken in clean medium to fine sands around and to the north of Moreton Island. *P. turkoroa* was only found once, in muddy sand in the south of Moreton Bay. None of these species co-occurred in samples.

Similar and consistent ecological separation is present for the five species of *Leptochelia* in Moreton Bay. Thus *L. myora* and *L. dijonesae* are littoral species, the former occurring amongst seagrasses, the latter amongst algae epiphytic on mangroves. Of the three sublittoral species, the abundant *L. opteros* (which does extend into the low littoral) inhabited epifaunal and algal habitats. The other two species were each only collected once, and associated with soft sediments: *L. karragarra* occurred in sandy sediments in the south of Moreton Bay, while *L. guduroo* was collected from sand with shell breccia at the northern end of Moreton Bay.

With the diversity and sympatricity of leptocheliid species present in Australian waters (see Appendix 1), it is deemed useful to offer an identification key to those species of the family described so far from Australia.

Key to adults of known Leptocheliidae of Australia

1. Antennule of four longer articles plus minute distal article. . . . . . . *Catenarius daviei**
— Antennule of three longer articles plus minute distal article. 2
— Antennule of more than six articles (males)*
. . . . 10

2. Carapace with posterior demarcation of second thoracomere; cheliped carpus distally extending into a cuff in which the propodus sits; antennule peduncle article 1 less than twice as long as wide; white with red markings in life. . . . . *Konarus cheiris**
— Carapace without posterior demarcation of second thoracomere; cheliped carpus distally normal; antennule peduncle article 1 at least 2.5 times as long as wide; without red markings in life. 3

3. Elongate distal setae on the cheliped merus pointing proximally in life, the longest as long as the merus; setose tubercles on pereopods 4–6. . . . . . . *Pseudoleptochelia fairgo*
— Less than four setae on cheliped merus, mostly shorter than article; no setose tubercles on pereopods 4–6.. 4

4. Uropod exopod of two segments; body olive green in life. . . . . . . *Leptochelia dijonesae*
— Uropod exopod of one segment; body colour other than green. 5

5. Uropod exopod only half length of proximal endopod segment.. 6
— Uropod exopod at least 0.8 times as long as proximal endopod segment. 7

6. Cephalon at least 1.5 times as long as wide; pereopod 1 basis <2.7 times as long as wide; antennule peduncle article 1 less than three times as long as wide. . . *Leptochelia myora*
— Cephalon less than 1.25 times as long as wide; pereopod 1 basis 3 times as long as wide; antennule peduncle article 1 more than three times as long as wide. . . . . *Leptochelia nobbi*

7. Longest distal seta on antennule peduncle article two twice as long as article; antenna peduncle with distal seta on article 3 longer than article, mid-length seta on article 4 exceeding distal tip of article. . . . . *Leptochelia guduroo**
— Longest distal seta on antennule peduncle article two less than 1.5 times as long as

article; antenna peduncle without distal seta on article 3, mid-length seta on article 4 as long as article width or absent. . . . . . . 8.

8. Uropod exopod as long as or longer than proximal endopod segment; cheliped carpus twice as long as wide; proximal article of antenna naked. 9
— Uropod exopod shorter than proximal endopod segment; cheliped carpus 1.6 times as long as wide; proximal article of antenna with small distal seta. . . . .
. . . . *Leptochelia opteros*

9. Uropod exopod as long as proximal endopod segment; dactylus plus claw on first pereopod as long as propodus; antennule peduncle article 2 longest distal seta much shorter than article length. . . . .
. . . . *Leptochelia karragarra*
— Uropod exopod longer than proximal endopod segment; dactylus plus claw on first pereopod 1.25 times as long as propodus; antennule peduncle article 2 longest distal seta much longer than article length. . . . .
. . . . *Leptochelia daggi*

10. Cheliped subchelate (*Pseudoleptochelia*).. 17
— Cheliped chelate. 11

11. Cheliped longer than body, merus rectangular; proximal antennule article longer than cephalon plus pereonite 1. . . . .
. . . . *Leptochelia vimesi* *
— Cheliped less than half body length; proximal antennule article about as long as cephalon.. 12

12. Pereopod 6 basis with distinct posterodorsal flange. . . . . . . *Leptochelia opteros*
— Pereopod 6 basis without flange, normal. .
. . . . 13

13. Cheliped carpus with convex dorsal edge and ventral flange, the whole thus being almost as wide as long; chela fixed finger set at right-angles to axis of propodus. . . .
. . . . *Leptochelia myora*
— Cheliped carpus at least 1.5 times as long as wide, without ventral flange; chela fixed finger generally set along same axis as propodus. 14

14. Uropod exopod of two segments. . . . . .
. . . . *Leptochelia dijonesae*
— Uropod exopod of one segment. 15

15. Chela fixed finger stout, shorter than body of propodus, without tooth-like apophyses

on cutting edge; antennule flagellum articulating anaxially on peduncle, proximal two articles much shorter than wide. . . . . . .
. . . . *Leptochelia nobbi*
— Chela fixed finger elongate, slender, with one or two tooth-like apophyses on cutting edge; antennule flagellum proximal articles as long as or longer than wide, articulating axially on peduncle. 16

16. Chela fixed finger shorter than body of propodus, with single tooth-like apophysis on cutting edge; uropod exopod as long as proximal segment of endopod, endopod of four segments; body length < 2 mm. . . . .
. . . . *Leptochelia karragarra*
— Chela fixed finger longer than body of propodus, with two tooth-like apophyses on cutting edge; uropod exopod shorter than proximal segment of endopod, endopod of five segments; body length > 3 mm. . . . .
. . . . *Leptochelia daggi*

17. Cheliped propodus ventrally with single, distal, rounded apophysis; carpus with midventral rounded apophysis.. . . . .
. . . . *Pseudoleptochelia fairgo*
— Cheliped propodus with mid-ventral rounded apophysis as well as ventrodistal, pointed apophysis; carpus without ventral apophysis. . . . . *Pseudoleptochelia straddi* *

* males of *Catenarius daviei*, *Konarus cheiris* and *Leptochelia guduroo* unknown. Females of *Leptochelia vimesi* and *Pseudoleptochelia straddi* unknown.

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APPENDIX 1

List of the species of Tanaidacea recorded from the waters of continental Australia, with their Australian provenance.

Order TANAIDACEA Dana, 1849

Suborder APSEUDOMORPHA Sieg, 1980
Superfamily Apseudoidea Leach 1814

Family **Apseudidae** Leach, 1814

Annexos abditospina Błażewicz-Paszkowycz & Bamber, 2007 — Vic, Tas
Apseudes atuini Bamber, 2005 — WA
Apseudes bucospinosus Guţu, 2006 — Qld
Apseudes poorei Błażewicz-Paszkowycz & Bamber, 2007 — Vic, Tas
Apseudes tuski Błażewicz-Paszkowycz & Bamber, 2007 — Vic
Bilobatus gallardoi — Shiino, 1963) — NT, WA
Bilobatus rostridentatus Guţu, 2006 — Qld
Androgynella fecunda Guţu, 2006 — NT
Muramurina splendida (Guţu, 2006) — Qld
Bunakenia (B.) salzella Bamber, 2005 — WA
Bunakenia (Extensibasella) anomala Guţu, 2006 — Qld
Gollumudes larakia (Edgar, 1997) — NT, Qld, Vic, Tas
Gutuapseudes manda Edgar, 1997 (? = *Apseudes*) — NT
Hainanius (?) immaculatus Guţu, 2006 — Qld
Pugiodactylus daicovicii Guţu, 2006 — Qld
Pugiodactylus syntomos Błażewicz-Paszkowycz & Bamber, 2007 — Vic, Tas
Spinosapseudes colobus Błażewicz-Paszkowycz & Bamber, 2007 — Vic, Tas

Family **Whiteleggiidae** Guţu, 1972

Pseudowhiteleggia typica Lang, 1970 — NSW, Vic, Tas
Whiteleggia multicarinata (Whitelegge, 1901) — NSW, Vic, Tas
Whiteleggia stephensoni Boesch, 1973 — Qld

Family **Kalliapseudidae** Lang, 1956

Kalliapseudes langi Guţu, 2006 — Qld
Kalliapseudes multiarticulus Guţu, 2006 — NT
Kalliapseudes struthi Bamber, 2005 — WA
Kalliapseudes obtusifrons (Haswell, 1882) — NSW
Cristapseudes unicus Guţu, 2006 — Qld
Transkalliapseudes banana sp. nov. — Qld
Transkalliapseudes spinulata Drumm & Heard, 2006 — WA

Family **Metapseudidae** Lang, 1970
Subfamily Metapseudinae Guţu, 1972

Labraxeudes heliodiscus Błażewicz-Paszkowycz & Bamber, 2007 — Vic
Metapseudes wilsoni Błażewicz-Paszkowycz & Bamber, 2007 — Vic
Pseudapseudomorpha wagait (Edgar, 1997) — NT

Subfamily Synapseudinae Guţu, 1972

Curtipleon loerzae sp. nov. — Qld
Synapseudes australianus Băcescu, 1981 — Qld

Family **Numbakullidae** Guţu & Heard, 2002

Numbakulla pygmaeus Guţu & Heard, 2002 — WA

Family **Parapseudidae** Guţu, 1981

Longiflagrum caeruleus (Boesch, 1973) — Qld
Longiflagrum aestuarius (Boesch, 1973) — Qld
Pakistanapseudes australianus Guţu, 2006 — Qld
Pakistanapseudes bassi Błażewicz-Paszkowycz & Bamber, 2007 — Vic
Pakistanapseudes perulpa Błażewicz-Paszkowycz & Bamber, 2007 — Qld
Pakistanapseudes ridculli Bamber, 2005 — WA
Pakistanapseudes turkoroa Błażewicz-Paszkowycz & Bamber, 2007 — Qld
Parapseudes latifrons agg. (Grube, 1864) — WA
Platylicoa setosa Guţu, 2006 — Qld
Pseudohalmyrapseudes aquadulcis Larsen & Hansknecht, 2004 — NT
Remexudes toompani Błażewicz-Paszkowycz & Bamber, 2007 — Qld, Vic
Saltipedis forex Bamber, 2005 — WA
Saltipedis incognita Bamber, 2005 — WA

Saltipedis nugoris Błażewicz-Paszkowycz & Bamber, 2007 — Vic

Family **Pagurapseudidae** Lang 1970
Subfamily Pagurapseudinae Lang, 1970

Pagurapseudes abrucei Băcescu, 1981 — Qld
Pagurapseudes spinipes Whitelegge, 1901 — NSW
Macrolabrum boeri Băcescu, 1981 — Qld
Macrolabrum impedimenta Bamber, 2005 — WA
Pagurotanais koonungai sp. nov. — Qld

Subfamily Hodometricinae Guţu, 1981

Hodometrica australis (Haswell, 1882) — NSW
Indoapseudes macabre Bamber, 2005 — WA
Similipedia diarris Błażewicz-Paszkowycz & Bamber, 2007 — Vic

Suborder NEOTANAIDOMORPHA Sieg, 1980

Family **Neotanaidae** Lang, 1956
Neotanais noelitaiti Larsen & Hansknecht, 2002 — Vic

Suborder TANAIDOMORPHA Sieg, 1980
Superfamily Tanaiodea Dana, 1849
Family **Tanaidae** Dana, 1849
Subfamily Sinelobinae Sieg, 1980

Sinelobus barretti Edgar, 2008
Sinelobus pinkenba sp. nov. — Qld
? *Sinelobus stanfordi* (Richardson, 1905) — Qld

Subfamily Pancolinae Sieg, 1980

Zeuxo (Zeuxo) angua Bamber, 2005 — WA
Zeuxo (Zeuxo) kirkmani Edgar, 2008 — WA
Zeuxo (Zeuxo) nannioggae Bamber, 2005 — WA
Zeuxo (Zeuxo) normani (Richardson, 1905) — NSW, Tas
Zeuxo (Zeuxo) odohertyae Edgar, 2008 — Tas
Zeuxo (Zeuxo) shepherdi Edgar, 2008 — SA
Zeuxo (Parazeuxo) amiti sp. nov. — Qld
Zeuxo (Parazeuxo) belli Edgar, 2008 — Qld
Zeuxo (Parazeuxo) mooneyi Edgar, 2008 — NSW
Zeuxo (Parazeuxo) russi Edgar, 2008 — Qld
Zeuxoides casamunda Bamber, 2005 — WA
Zeuxoides lasti Edgar, 2008 — Tas
Zeuxoides lauriebourqueae Edgar, 2008 — WA
Zeuxoides mawbeyi Edgar, 2008 — Tas
Aviatanais tempestacera Bamber, 2005 — WA
Hexapleomera cf. *robusta* (Moore, 1894) — Qld
Pancoloides moverleyi Edgar, 2008 — Tas

Subfamily Tanainae Dana, 1849

Anstrotanais rileyi Edgar, 2008 — WA, Tas
Tanais cf. *dulongii* (Audouin, 1826) — WA
Tanais pongo Bamber, 2005 — WA

Superfamily Paratanaoidea Lang, 1949

Family **Anarthruridae** Lang 1971
Subfamily Anarthrurinae Lang, 1971
Agathotanais spinipoda Larsen, 1999 — Vic

Subfamily Leptognathiinae Sieg, 1976

Tanaopsis canaipa sp. nov. — Qld

Subfamily Akanthophoreinae Sieg, 1986

Araphura io Bamber, 2005 — WA
Collettea cylindratoides Larsen, 2000 — Vic
Tanaella dongo Bamber, 2005 — WA
Tangalooma rous gen. et sp. nov. — Qld

Family **Typhlotanaidae** Sieg, 1984

Antiplotanais coochiundlo gen. et sp. nov. — Qld
Antiplotanais lutze (Bamber, 2005) — WA

Family **Paratanaidae** Lang, 1949

Subfamily Bathytanaidinae Larsen & Heard, 2001

Bathytanais bathybrotes (Beddard, 1886) — Qld, NSW
Bathytanais arcuamans Larsen & Heard, 2001 — WA
Bathytanais culteriformis Larsen & Heard, 2001 — Qld, WA
Bathytanais fragilis Larsen & Heard, 2001 — Vic
Bathytanais greebo Bamber, 2005 — WA
Bathytanais juergeni Larsen & Wilson, 1998 — Qld, NSW

Pseudobathytanais gibberosus Larsen & Heard, 2001 — Vic

Subfamily Teleotanaidinae nom. nov.

Teleotanais warragamba sp. nov. — Qld

Subfamily Paratanaidinae Lang, 1949

Paratanais gaspodei Bamber, 2005 — WA
Paratanais maleficus Larsen, 2001 — NSW
Paratanais malignus Larsen, 2001 — NSW
Paratanais perturbatins Larsen, 2001 — NSW
Paratanais vetinari Bamber, 2005 — WA
Paratanais wanga sp. nov. — Qld
Xeplenois anemos Bamber, 2005 — WA

Family **Leptocheliidae** Lang 1973

Leptochelia daggi Bamber, 2005 — WA
Leptochelia dijonesae sp. nov. — Qld
Leptochelia guduroo sp. nov. — Qld
Leptochelia karragarra sp. nov. — Qld
Leptochelia myora sp. nov. — Qld
Leptochelia nobbi Bamber, 2005 — WA
Leptochelia opteros sp. nov. — Qld
Leptochelia vimesi Bamber, 2005 — WA
Catenarius daviei gen. et sp. nov. — Qld
Pseudoleptochelia fairgo Bamber, 2005 — WA, Qld
Pseudoleptochelia straddi sp. nov. — Qld
Konarus cheiris Bamber, 2006 — Qld

Family **Pseudotanaidae** Sieg, 1973

Subfamily Pseudotanainae Sieg, 1973
Pseudotanais (Akanthinotanais) scrappi Bamber, 2005 — WA

Phycomenes zostericola gen. nov, sp. nov., a new pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from Moreton Bay, Queensland

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ABSTRACT

A new genus and species of Australian pontoniine shrimp, *Phycomenes zostericola*, is described and illustrated. The genus is closely related to *Periclimenes* Costa, and distinguishable by the presence of a triangular median process on the fourth thoracic sternite. The new species appears common in sea grass habitats along eastern and northern Australia. ❑ *Crustacea, Decapoda, Pontoniinae, Phycomenes, new genus, new species, Australia, sea grass.*

The study of the pontoniine shrimp fauna of Moreton Bay, south east Queensland, commenced with the investigation of coral symbionts at Myora, South Stradbroke Island, by Patton (1966), who reported the presence of five species. The fauna now comprises 23 species, most of which are from the northern half. None have been previously reported from the southern half of Moreton Bay.

In December 2005 and February, 2006, the Centre for Aquatic Processes and Pollution, Griffith University, carried out a faunistic survey as part of a project to study the importance of edge effects in seagrass landscapes at the mouth of Loder's Creek, an outflow into the Gold Coast Broadwater, in south eastern Queensland, under the direction of Dr Rod Connolly. Numbers of a small pontoniine shrimp were collected and some provided for taxonomic study. Although very *Periclimenes*-like, they could not be identified with any known species of that genus. Further examination indicated that they could not be satisfactorily placed in of the described genera and a new genus is now designated for their inclusion. A number of similar shrimps from other localities outside Australia are currently

under going study and are likely to be also referred to this genus.

The type material is deposited in the collections of the Queensland Museum (QM), Muséum National d'Histoire naturelle, Paris (MNHN); Northern Territory Museum, Darwin, (NTM); Nationaal Natuurhistorisch Museum-Naturalis, Leiden, (RMNH); National Museum of Natural History, Washington (USNM). Other abbreviations used are: CL, postorbital carapace length.

SYSTEMATICS

Sub-phylum Crustacea
Order Decapoda Latreille, 1802
Family Palaemonidae Rafinesque, 1815
Sub-family Pontoniinae Kingsley, 1878

Phycomenes gen. nov.

Diagnosis. Small sized pontoniine shrimps of slender subcylindrical body shape. Carapace smooth, glabrous, with rostrum well developed, dorsally and ventrally dentate, lateral carinae feebly developed, ventral carina obsolete, epigastric spine present, hepatic and antennal spines present, hepatic spine fixed, supraorbital spines absent, orbit poorly developed, without

postorbital groove, inferior orbital angle strongly produced, rounded, with feeble ventral flange, anterolateral, angle of branchiostegite not produced; abdomen normally developed, smooth, glabrous, third segment not posterodorsally produced, non-carinate, pleura rounded, fourth and fifth not acutely produced posteriorly, sixth segment not elongate, normal, with distolateral angle produced, antenna with stylocerite acute, statocyst normal; flagella well developed; antennal basicerite with ventrolateral tooth, scaphocerite well developed, with strong distolateral tooth not exceeding distal lamella; ophthalmic somite with small subacute *béc ocellaire* and median pigment spot; eye well developed, stalk subcylindrical, cornea globular, well pigmented, with conspicuous accessory pigment spot, stalk without proximolateral articular process; epistome unarmed, with small submedian hemispherical bosses, without anteromedian process; mandible without palp, molar and incisor processes normal; maxillula with feebly bilobed palp; maxilla normal, with simple palp, basal endite bilobed, coxal endite convex, obsolescent, first maxilliped with simple non-setose palp, basal and coxal endites feebly separate, broad, exopod with slender flagellum, caridean lobe elongate, epipod small, rounded; second maxilliped with normal endopod, exopod slender, epipod suboval, without podobranch; third maxilliped slender, ischiomerus feebly separated from basis, exopod slender, coxa with elongate lateral plate, without arthrobranch, maxillipedal exopods generally with four plumose terminal setae; second to third thoracic sternites not elongate, unarmed, fourth with acute transverse median process; with five pleurobranchs; first pereiopods short, slender, chela with fingers simple, cutting edges entire, coxa with small setose distoventral process; second pereiopods feebly developed, slender, subequal and similar; chela slender, fingers subequal to palm length, without molar process and fossa; cutting edges unarmed, slightly gaping proximally, merus without distoventral tooth, ambulatory pereiopods slender, dactyls slender, biunguiculate, without basal process, merus and ischium distinct; uropod with protopodite bluntly produced; exopod with small distolateral tooth, with small mobile spine; telson with two pairs of small dorsal spines, three pairs of posterior spines.

Type species: *Phycomenes zostericola* sp. nov., by present designation and monotypy.
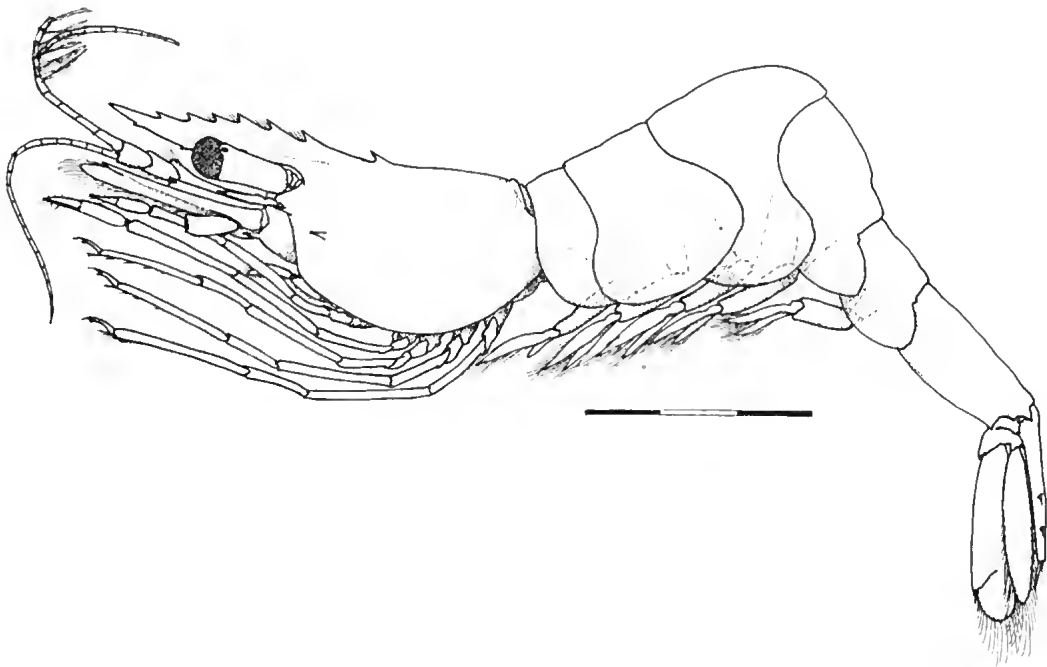

FIG. 1. *Phycomenes zostericola* gen. nov., sp. nov., holotype, post-ovigerous female, Loder's Creek, Qld (QM-W28406). Scale bar in millimetres.

Etymology. From *phycus*, (Latin), sea-weed, a reference to the habitat of this shrimp, and *-menes*, from part of *Periclimenes*, a pontoniine generic name first used by Costa, 1844. Gender masculine.

Systematic Position. In its general morphology *Phycomenes* appears most closely related to the species of *Periclimenes* Costa, 1844, that are generally referred to as the *Periclimenes obscurus* species group, presently including about 12 species (Bruce 1987). *Phycomenes* differs from all these in the presence of a distinct acute transverse median process on the fourth thoracic sternite. Such a character is absent from the majority of pontoniine genera and is known only in the genera *Eupontonia* Bruce, *Exoclimenella* Bruce, *Harpilius* Dana, *Kemponia* Bruce, *Palaemonella* Dana, *Periclimenella* Bruce, *Philarius* Holthuis, and *Vir* Holthuis. This process is also present in a number of palaemonine genera and can be considered as a plesiomorphic character. The species of these genera all have well developed second pereiopods with relatively large chelae and also the ambulatory dactyls in all these genera are simple. In contrast, *Phycomenes* has remarkably poorly developed second pereiopods and ambulatory dactyls that are distinctly biunguiculate.

Most of the mouthparts of *P. amethysteus* (Risso, 1816), the type species of the genus *Periclimenes* Costa, 1844, have been illustrated by Holthuis (1952, fig. 4). Those of *Phycocaris* gen. nov. show a close resemblance. The principal difference is that the epipod of the first maxilliped is small, simple and rounded in *Phycocaris* and larger, and distinctly bilobed in *P. amethysteus*. The maxillipedal flagella are also provided with numerous long plumose setae (about 12–15) in *P. amethysteus* (see Holthuis, 1952, fig. 4ef) in contrast to *Phycomenes*, in which only four terminal plumose setae are present.

With the removal of *Harpilius* Dana and *Kemponia* Bruce (Bruce 2004) from the genus *Periclimenes* Costa, the definition of the genus given by Bruce (1994), which states the fourth thoracic sternite may possess or lack a median process, is no longer correct. *Periclimenes amethysteus*, the type species, does not have a well developed acute median process on the fourth thoracic sternite, but has a distinct ven-

tral rostral carina and well developed second pereiopods with robust chelae. *Periclimenes* s. str. should be restricted to species without a well developed median fourth sternal process. Of the species remaining in *Periclimenes* s. str. none are known to have such a process, although the morphology of this sternite for some species presently included has yet to be reported.

Phycomenes also shares several features with the species of the *Periclimenes aesopius* species group, particularly the small ventral flange of the inferior orbital angle, a feature otherwise so far only reported in this group. The general form of the well developed rostrum, devoid of a ventral carina, and the ambulatory pereiopods are also particularly similar, but *aesopius* group species all have well develop second pereiopod chelae.

It may be noted that Menon (1939) described the larval stages of *Perclimenes indicus* Kemp, 1922, a closely related species with which the present species had been earlier confused. He remarked that, in comparison with some other species of the genus, 'some of the differences which the present species exhibit ... seem large enough to render its position within the genus somewhat doubtful.'

Phycomenes zostericola sp. nov.
(Figs 1–7)

Periclimenes indicus (in part) — Bruce, 1977: 226–228, figs 32–33.

? *Periclimenes (P.) nr obscurus* — Wadley, 1978: 19, fig. 9k; Young & Wadley, 1979: 86, tab.2.

Periclimenes indicus — Bruce & Coombes, 1995: 131; Bruce & Coombes, 1997: 313–314; Davie, 2002: 328.

Material Examined. HOLOTYPE: QM-W28406, ♀, Loder's Creek, Labrador, Qld, 11.2007, J. Haig. PARATYPES: QM-W28270, 4 ovig. ♀, RMNH-D51761, ♂, ovig. ♀; MNHN-Na16606 ♂, ovig. ♀; NTM-Cr015502, 2 ovig. ♀; USNM-1102691, 2 ovig. ♀, same data as for holotype.

OTHER MATERIAL: NTM-Cr009238, 25 spms (10 ovig. ♀), Costen's Point, Port Hacking, NSW, from *Posidonia* beds, 13.07.1976, V. Wadley. NTM-Cr009239, 39 spms (28 ovig. ♀), Costen's Point, Port Hacking, NSW, from *Posidonia* beds, 13.07.1976, V. Wadley. QM, 3 ♂ , 10 ovig. ♀, AJB #3425, mouth of Loder's Creek, Broadwater, Gold Coast, in sea-grass, hand net, 1–1.5m, 15–18.12.2005, H. Moller. RMNH, 3 ♀ (2 ovig.), Myora, North Stradbroke Is., Qld, shallow
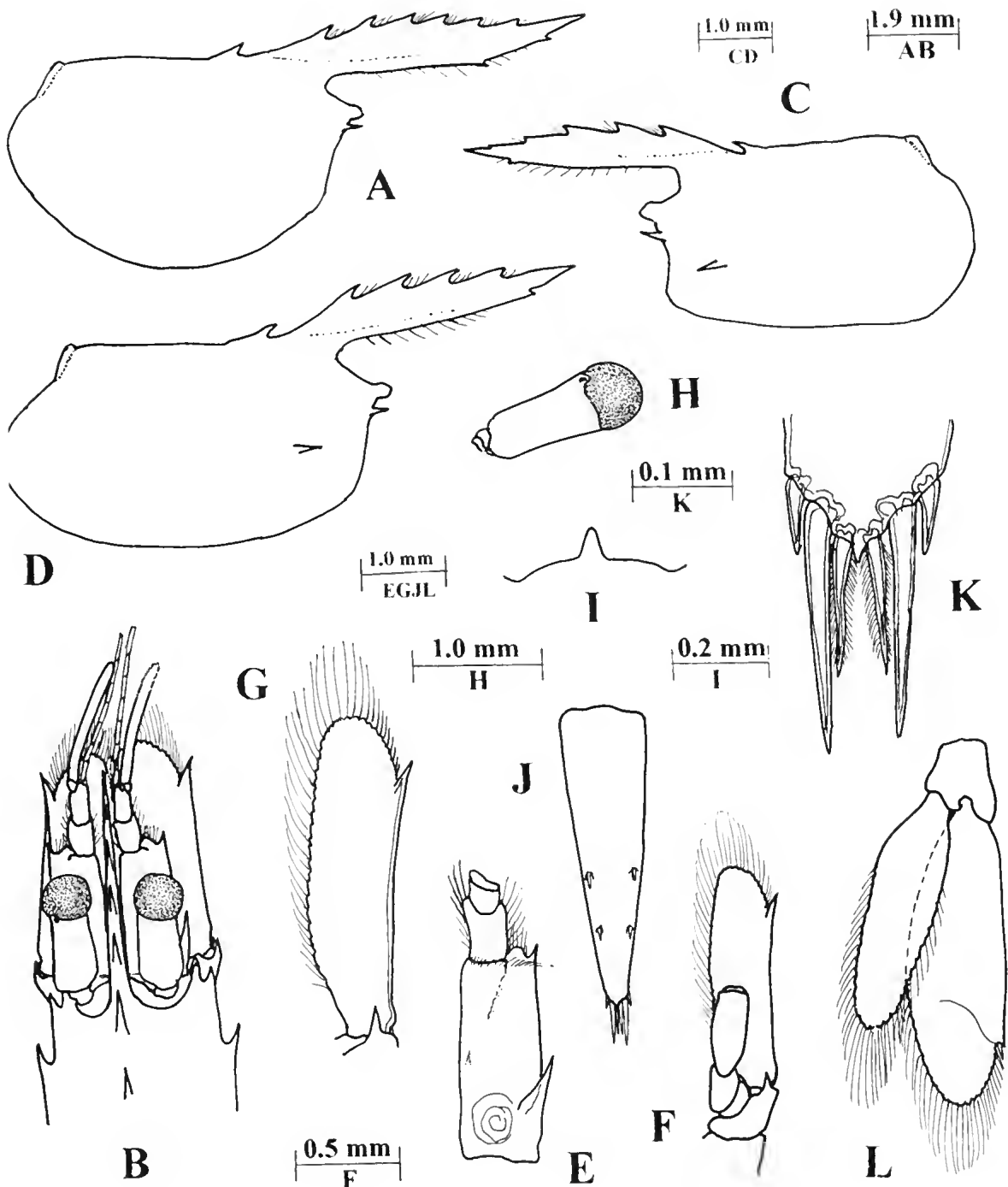
FIG. 2. *Phycomenes zostericola* gen. nov., sp. nov., paratype, S, Loder's Creek, SE Qld (QM-W28270). A, carapace and rostrum. B, anterior carapace and appendages, dorsal. C, carapace and rostrum. D, same. E, antennule. F, antenna, ventral. G, scaphocerite. H, eye. I, fourth thoracic sternite. J, telson. K, same, posterior spines. L, uropod. A, B=ovigerous female; E–L= males.

sublittoral, 31.01.1968, A.J. Bruce. QM W28352, 1 spec., bopyridized, Loder's Creek, Labrador, Qld, 1.0 m, Sept. 2007, J. Haig. QM-W28478, 4 ♂, 14 ♀ (13 ovig.), Myora, North Stradbroke Is., Qld, shallow sublittoral, 31.01.1968, A.J. Bruce. QM-W28479, 2 ovig. ♀, Peel Island, Moreton Bay, Qld, shallow sublittoral, in *Sargassum*, 23.09.1968, A.J. Bruce. QM-W24039, 2 specs, Fisherman Island, nr mouth of Brisbane R., Moreton Bay, 27°22'S, 153°10'E, 0.2–0.5 m, sand/mud flat, pools, symbiotic with seagrass, *Zostera capricorni*, 2–4.06.1998, netted, P. Davie, J.W. Short. QM-W17139, 5 spms, Fishermen Is., 27°23'S, 153°10'E, 2 m, seagrass, 23 .07. 1990, trawled, Queensland Fisheries Service. QM-W18190, 10 spms, Starcke R. mouth, 14°47.1'S, 145°01'E, 1m, *Zostera* seagrass, 12.11.1992, netted, P. Davie, J.W. Short. QM-W25489, 52 spms, Dunwich, North Stradbroke Is., Moreton Bay, 27°30'S, 153°24'E, near anemone, *Stichodactyla haddoni*, 10.09.2000, W.K. Patton. NTM-Cr006496, 11 spms (9 ovig. ♀), stn CP/13/2, Coral Bay, Port Essington, Arnhem Land, NT, from *Sargassum* washings, 0.5 m, 20 .07. 1981, A.J. Bruce. NTM-Cr001197 1, ♂, 2 ovig.♀, stn CP/10, Black Point, Port Essington, Arnhem Land, NT,18.07.1981, 1–2m, A. J. Bruce & J.N.A. Hooper. NTM-Cr008241, 2 ovig.♀, stn CP/18, Midjari Point, Cobourg Peninsula, Arnhem Land, NT, low water spring tide, 16.10.1981, A.J. Bruce *et al.*; NTM-Cr009285, 2 ovig. ♀, 1 juv., stn CP/58, Caiman Creek, Port Essington, Arnhem Land, NT, <1m, 15.05.1983, N.L. Bruce & A.J. Bruce. QM-W21326, 3 spms, unnamed peninsula SE of Cape Londonderry, Kimberley Coast, 13°45.3'S, 126°48.5E, 1.5 m, marine, fringing reef, symbiotic with mac-rophyte, *Sargassum*, 28.11.1995, netted, J.W. Short.

Description. Slenderly built shrimps (Fig. 1), of subcylindrical body form.

Rostrum: (Figs 2A–D, 5A) well developed, slender, straight, horizontal, 0.9 of CL (♂), subequal to CL (♀), distally acute, slightly exceeding antennular peduncle, dorsal carina well developed, deepest at about half length, with 4–6 (♂), 5–6 (♀) acute teeth, all pre-orbital, first to third or fourth teeth well developed, distal teeth diminishing, sometimes minute (Fig. 5B), interdental spaces with short plumose setae, lateral carinae obsolescent, ventral carina obsolete, ventral margin straight, with 1–2 (one specimen with 3) well spaced small acute distal teeth, with median row of short plumose setae.

Carapace: (Fig. 2A–C) smooth, glabrous, with non-articulate epigastric spine, at about 0.7 of CL, lacking supraorbital spine, orbit feebly developed, antennal spine well developed, marginal, exceeding inferior orbital angle in female, subequal in male, inferior orbital angle (Fig. 5C–D) broad, bluntly produced in dorsal and lateral views, hepatic spine well developed, subequal to antennal spine, on slightly lower level, at about 0.85 of CL, anterolateral branchiostegite bluntly obtuse.

Abdomen: without special features; third tergite without posterior marginal denticulations, sixth segment about 0.75 of CL, 2.3 times longer than deep, 1.9 times length of fifth segment, compressed, posterolateral angle well developed, acute, posteroventral similar, pleura of first three segments broadly rounded, fourth and fifth posteriorly produced, bluntly rounded.

Telson: (Fig. 2J) about 0.8 of CL, about 3.4 times longer than anterior width, lateral margins sublinear, posteriorly convergent, with two pairs of subequal dorsal spines, about 0.06 of telson length, at 0.56 and 0.73 of telson length, posterior margin (Fig. 2K) about 0.25 of anterior width, angular, with small acute median process, lateral telson spines small, similar to dorsal spines, intermediate spines robust, about 0.15 of telson length, submedian spines slender, subventral, feebly setulose, about 0.45 of intermediate spine length.

Antennule: (Fig. 2E) with peduncle about 0.75 of CL, proximal segment about 2.48 times longer than central width, medial margin straight with well developed small acute ventral tooth at 0.5 of length, distolateral angle produced (Fig. 5E), rounded, slightly exceeding acute distolateral tooth, anterior margin setose, with long slender plumose setae, lateral margin straight, stylocerite acute, reaching about 0.5 of medial margin length, statocyst normal; intermediate and distal segments short, subequal in length, combined length about 0.6 of proximal segment length, intermediate segment with numerous plumose setae medially and laterally, upper flagellum with proximal 5–6 segments fused, shorter ramus with 2–3 segments, with about 5 groups of aesthetascs, longer ramus filiform.

Antenna: (Fig. 2F) without antennal gland tubercle medially, basicerite with slender acute ventrolateral tooth, carpocerite subcylindrical, short, about 2.3 times longer than wide, reaching to about 0.45 of scaphocerite length, merocerite and ischiocerite normal, short; scaphocerite (Fig. 2G) well developed, well exceeding antennular peduncle and rostral tip, lamella narrow, broad-
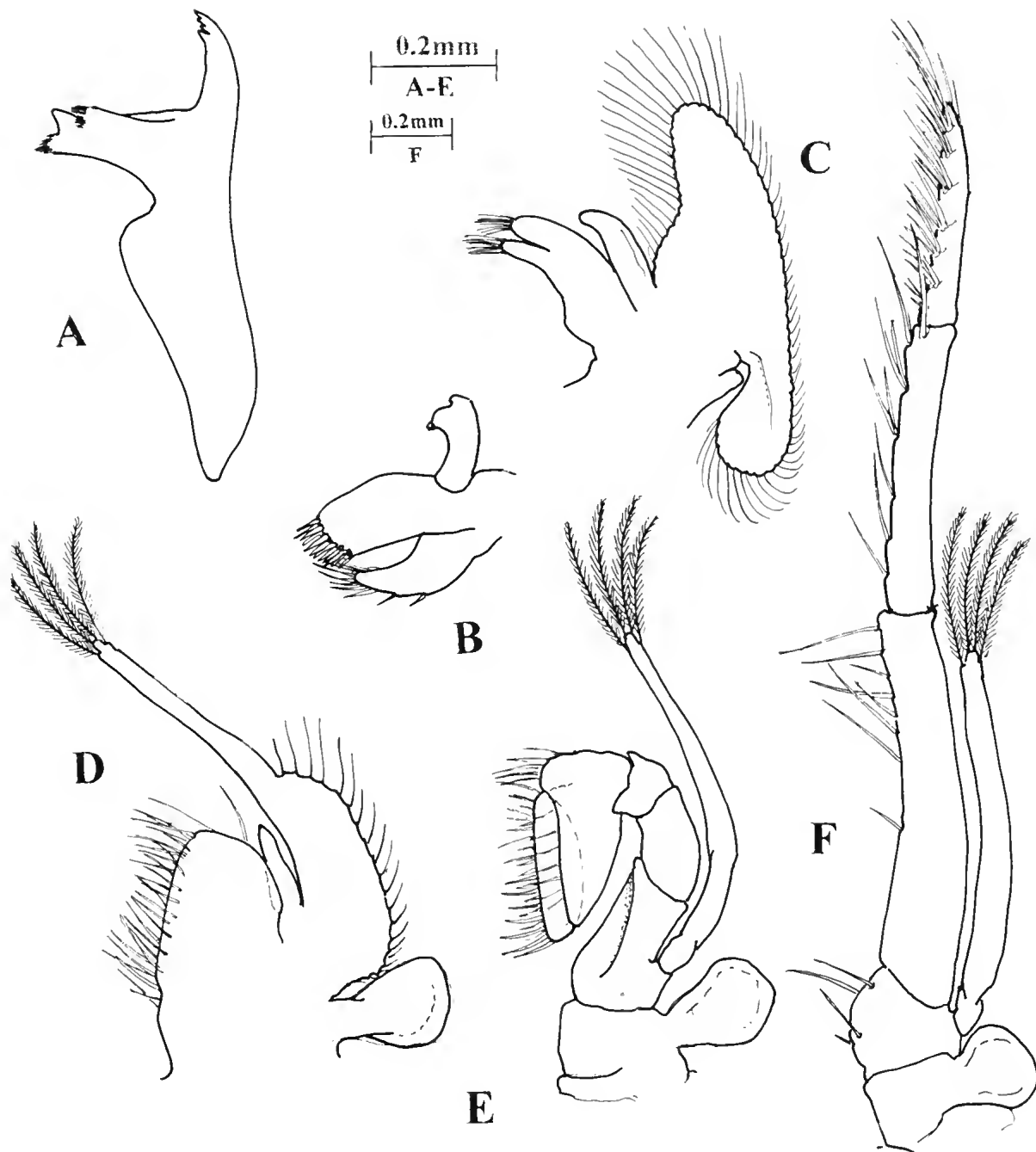
FIG. 3. *Phycomenes zostericola* gen. nov., sp. nov., male, paratype, Loder's Creek, SE Qld (QM-W28270). A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped. A, B, D–F= male CL 2.0 mm, C= ovigerous female paratype, CL 2.8 mm.

ly rounded distally, about 3.8 times longer than central width, lateral margin feebly concave, with well developed, slender acute tooth distally, about 0.09 of scaphocerite length, at 0.8 of lateral margin length, well short of distal margin of lamella.

Ophthalmic somite: with small subacute *béc ocellaire* and median pigment spot.

Eye (Fig. 2H) about 0.45 of CL, with well pigmented globular cornea, with distinct dorsal accessory pigment spot, diameter about 0.2 of CL, stalk about twice as long as wide, length about 1.7 times corneal diameter, without distodorsal tubercle.

Epistome without anteromedian spine, with small hemispherical bosses laterally.

Mandible: (Fig. 3A) robust, without palp, right molar process stout, subcylindrical, distally oblique with pair of blunt teeth posteriorly, separated by tuft of short setae from anterior pair of blunt teeth, incisor process (Fig. 5H–1) normal, tapering distally, with 3 or 4 small acute teeth distally, medial and lateral teeth larger than inner teeth, medial margin without denticles.

Maxillula: (Fig. 3B) with feebly bilobed palp (Fig. 5J), upper lobe slender, non-setose, lower lobe with small simple terminal setose tubercle, upper lacinia short, broad, distally truncate, with about 12 short stout similar simple spines and numerous spiniform setae, lower lacinia short, tapering, with numerous longer spiniform feebly setulose setae distally, two small spinules ventrally.

Maxilla: (Fig. 3C) with simple flattened non-setose palp, about 4.5 times longer than basal width, basal endite bilobed, lobes short, distal lobe more robust with about 6 simple setae distally, proximal lobe smaller and shorter, with about 4 distal setae, coxal endite obsolete, margin feebly convex, scaphognathite normal, anterior lobe 1.4 times longer than width, medial margin emarginate, posterior lobe small, about 0.66 of length of anterior lobe, 2.4 times longer than basal width.

First maxilliped: (Fig. 3D) with palp short, similar to that of maxilla, non-setose, basal endite well developed, almost fully fused with coxal endite, distal margin rounded, medial border straight, densely setose with simple slender spiniform setae, coxal endite separated from basal by small notch, feebly convex, sparsely setose, exopod normal, with robust flagellum with 4 plumose terminal setae, caridean lobe well developed, narrow, epipod small, rounded.

Second maxilliped: (Fig. 3E) of normal form, dactylar segment about 3.4 times longer than broad, with serrulate medial spines, longest distally, propodal segment slightly produced anteromedially, with few spiniform setae, carpus, merus and ischiobasis without special features, exopod with robust flagellum with 4 plumose terminal setae, coxa not medially produced, non-setose, epipod small, rounded, without podobranch.

Third maxilliped: (Fig. 3F) reaching to exceed carpocerite by length of terminal segment, with ischiomerus not fused to basis, combined segment slender, tapering slightly distally, about 6.2 times longer than central width, medial margin sparsely setose, lateral margin non-setose, penultimate segment 0.7 of antepenultimat segment length, subcylindrical, 8.0 times longer than wide, several groups of finely serrulate spiniform setae medially, terminal segment about 0.8 of penultimate segment length, 5.5 times longer than basal width, tapering distally, with long terminal spine, numerous groups of finely serrulate spiniform setae medially; basis medially convex, sparsely setose, exopod with robust flagellum, not reaching distal end of ischiomerus, with four plumose terminal setae, coxa not produced, with semicircular lateral plate, without arthrobranch.

Thoracic sternites: with first narrow, second and third widening, fourth (Fig. 2I) broad with stout median conoidal process, posterior sternites broad, unarmed.

First pereiopod: (Fig. 4A) slender, slightly exceeding antennular peduncle, to distolateral scaphocerite spine, chela (Fig. 4B) with palm oval in section, slightly compressed, about 1.7 times as long as deep, with sparse rows of short transverse cleaning proximally, fingers with numerous tufts of setae, about 0.8 of palm length, stout, with simple hooked tips, cutting edges lateral, entire; carpus slender, about 1.45 times chela length, 5.0 times longer than distal width, tapering proximally, with few serrulate cleaning

setae distoventrally; merus subequal to carpal length, about 7.0 times longer than central width, uniform; ischium about 0.7 of chela length; basis and coxa without special features, coxa with small setose distomedial process with several simple setae.

Second pereiopods: (Fig. 4C) very poorly developed, only slightly larger than first pereiopods, short, subequal and similar, extending to exceed scaphocerite by about half length of fingers, all segments smooth, glabrous, chela (Fig. 4D) small, about 0.4 of CL, 1.35 times length of first pereiopod chela, palm about 2.5 times longer than central depth, subcylindrical, oval in section, fingers (Fig. 4E) 0.95 of palm length, sparsely setose; dactyl slender, about 5.7 times longer than proximal depth, dorsal margin feebly convex, with small acute hooked tip, cutting edge distally entire, proximal cutting edge unarmed, slightly gaping, fixed finger similar, unarmed or with single obsolescent denticle at about 0.33 of length, carpus short, about 1.1 times chela length, 7.0 times longer than distal width, tapering slightly proximally, unarmed; merus about 0.9 of carpus length, slender, 7.0 times longer than central depth, ischium about 1.15 of meral length, 8.5 times longer than distal width, tapering proximally, basis and coxa normal, without special features.

Ambulatory pereiopods: similar, moderately slender, third (Fig. 4F) extending to distolateral spine of scaphocerite, dactylus (Fig. 4H) about 0.3 of propod length, compressed, slender with well demarcated unguis, unguis slender, curved, about 8.5 times longer than basal width, subequal to length of dorsal margin of corpus, corpus about 3.0 times longer than maximal depth, dorsal margin feebly convex, ventral margin sinuous, with well developed distoventral tooth, about 0.45 of unguis length, 3.5 times longer than basal width; propod (Fig. 4G) about 0.5 of CL, about 14.0 times longer than central depth, uniform, with pair of simple distoventral spines, about 0.33 of dactylar corpus length, with similar pair and single spines at 0.85, 0.74 and 0.55 of length; carpus 0.5 of propod length, 7.0 times longer than distal width, tapering slightly proximally, unarmed; merus subequal to propod length, 10.0 times longer than wide, uniform; ischium about 0.6 of propod length, 8.5 times

longer than distal width, tapering proximally; basis and coxa without special features. Propods of fourth (Fig. 4I) and fifth pereiopods (Fig. 4J) slightly longer than third. Fifth pereiopod with numerous spinulate setae distoventrally.

Male first pleopod (Fig. 5K): with basipodite 2.5 times longer than wide; exopod about 1.1 times basipodite length; endopod (Fig. 5L) distally expanded, rounded, non-setose, 2.6 times longer than greatest width, with small elongate medial lobe, without cincinnuli

Male second pleopod (Fig. 5M): with basipodite 1.2 times longer than first pleopod, 2.6 times longer than central width; exopod about 1.3 times basipodite length, endopod 1.2 times basipodite length, with appendices (Fig. 5N) at about 0.45 of medial margin length, appendix masculina subcylindrical, about 3.5 times longer than width, 0.3 of endopod length, with 3 slender simple terminal spines, row of 4 similar spines ventrally of diminishing size proximally.

Uropod (Fig. 2L): with protopod distolaterally acute, rami well exceeding telson tip. exopod 3.1 times longer than broad, with lateral margin straight, with small acute distolateral tooth (Fig. 5O) with mobile spine medially, about 3.0 times tooth length, dieresis incomplete, well developed laterally, endopod about 0.85 of exopod length, 3.4 times longer than broad.

Ova: numerous, small, about 50.

Measurements. Holotype female, carapace and rostrum, 5.5 mm; postorbital carapace, 2.4 mm; total body length c.16.0 mm; second pereiopod chelae, 0.95 mm. Length of ovum, 0.5 mm.

Colouration. (Fig. 7AB). (From Bruce 1977). Generally transparent but mottled with red-brown, especially along ventral aspect of body, and dorsally over posterior margins of third and fourth abdominal segments, tip of scaphocerite, ventral eyestalk, coxae of pereiopods and tips of caudal fan. Scattered small white dots over branchiostegite and pleura. Ovary and ova bright green.

Etymology. From *zoster* (Latin), the generic name of the seagrass habitat of this species, and *–cola* (Latin), a dweller in.

Ecology. The Loder's Creek specimens were all collected from sweepings of *Zostera capricorni* Ascherson, 1876, in shallow water, with a salinity of 29–35 ‰. All 18 specimens from Myora
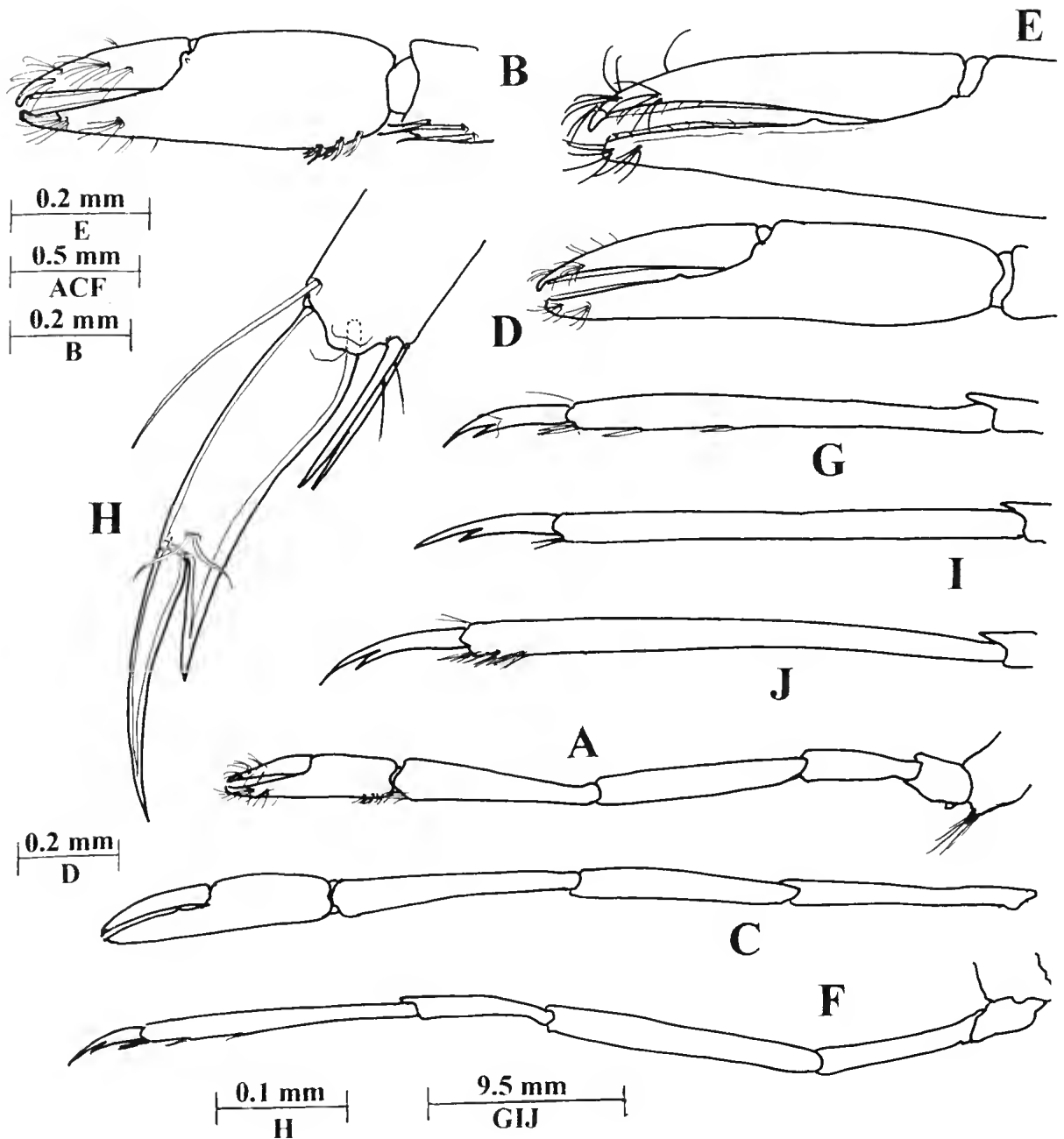
FIG. 4. *Phycomenes zostericola* gen. nov., sp. nov., male, paratype, Loder's Creek, Qld. (QM-W28270). A, first pereiopod. B, same, chela. C, second pereiopod. D, same, chela. E, same fingers. F, third pereiopod. G, same, propod and dactyl. H, same, distal propod and dactyl. I, fourth pereiopod, propod and dactyl. J, fifth pereiopod, propod and dactyl.
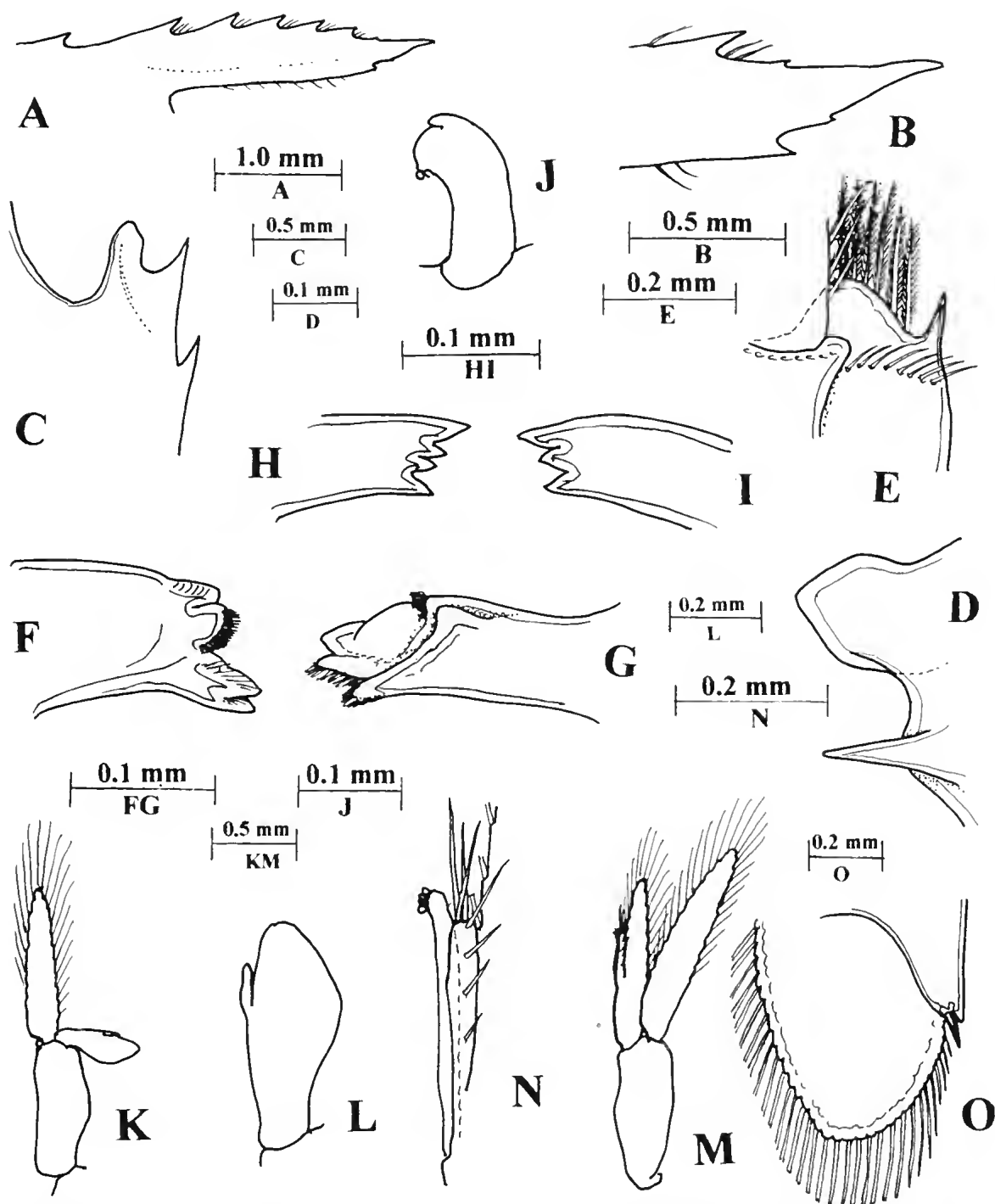
FIG. 5. *Phycomenes zostericola* gen. nov., sp. nov., male, paratype, Loder's Creek, SE Qld (QM-W28270). A, rostrum. B, same, tip. C, right orbital region, dorsal. D, left inferior orbital angle, lateral. E, antennule, proximal segment, distolateral angle. F, right mandible, molar process, dorsal aspect. G, same, ventral aspect. H, same, right incisor process. I, same, left process. J, maxillula, palp. K, first pleopod. L, same, endopod. M, second pleopod. N, same, endopod, appendix interna and appendix masculina. O, uropod, exopod, distolateral angle. A–J, O = ovigerous female. K–M = male.
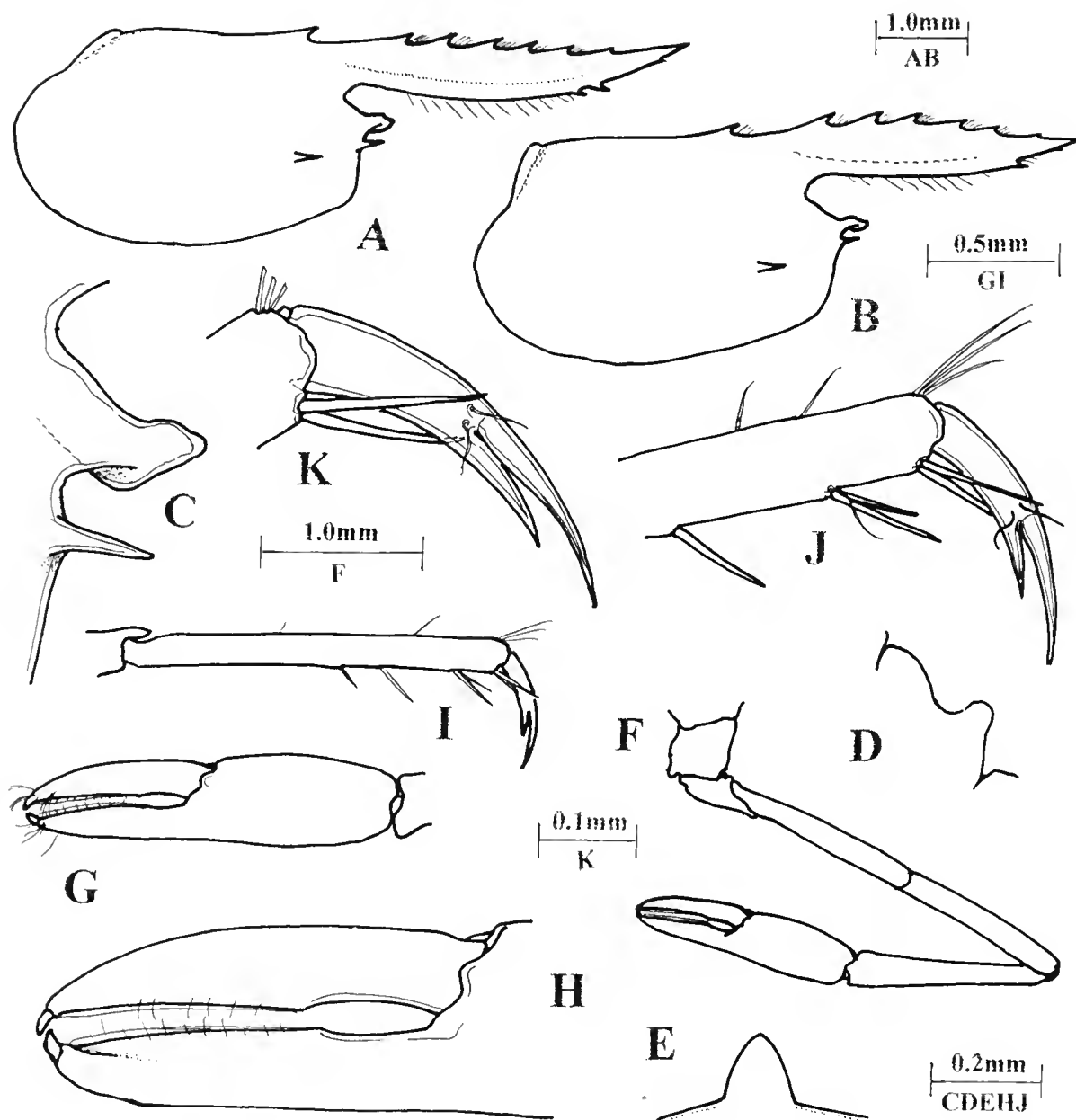
FIG. 6. *Phycomenes zostericola* gen. nov., sp. nov., ovigerous females, Peel Island, Qld (QM-W28479). A, B, carapace and rostrum. C, inferior orbital angle. D, ophthalmic somite profile. E, fourth thoracic sternite. F, second pereiopod. G, same, chela. H, same, fingers. I, third pereiopod, propod and dactyl. J, same, distal propod and dactyl. K, same dactyl.

were collected from a single specimen of the anemone *Macrodactylus doreensis* (Quoy & Gaimard), whereas the 52 specimens collected by Patton in 2000 were associated with another anemone, *Stichodactyla haddoni* (Saville-Kent).

Parasites. The Loders Creek specimen (QM-W28352) has a hemiarthrinid bopyrid, *Diplophryxus* sp. nov. (QM W28355), attached to the ventral abdomen (det. J. Markham, pers. comm.).

Distribution. Reported from New South Wales, Queensland, Northern Territory and northern Western Australia.

Remarks. The Loder's Creek material had all been frozen prior to preservation and specimens are rather macerated and in a fragile state.

Phycomenes zostericola is readily distinguished from *Periclimenes indicus* Kemp, 1915, with which it has been confused, by the absence of a series of robust distolateral spines on the merus of the third maxilliped, which are well developed in the latter species.

The two ovigerous female specimens from Peel island (Fig. 6) are referred to *Phycomenes zostericola* with some reservation. The larger specimen, CL 2.7 mm, has the rostrum slightly shorter than the CL, but in the smaller, CL 2.3 mm, it is distinctly longer, about 1.3 times the CL, with a preterminal ventral tooth and two ventral teeth at about 0.66 of the ventral length. Both have an epigastric tooth and six dorsal rostral teeth. The inferior orbital angle is more strongly produced, more acute and less rounded and with a more strongly developed ventral flange. The ophthalmic somite has a small rounded *béc ocellaire*. The median process of the fourth thoracic sternite is broader than in the type specimens. The second pereiopod chelae have the distal two thirds of the cutting edges entire with the proximal third slightly concave, forming a small diastema when closed. The third pereiopod dactyl has the accessory tooth more than half the length of the unguis and the distoventral spines of the propod well over half, about 0.8, of the dactylar corpus length; propod more robust, about 10 times longer than deep, 3.2 times longer than dactyl length. These differences suggest either that there may be substantial variation in this species or that two taxa may be involved but their existence in such close proximity reduces this possibility.

The recently collected specimens of *Phycomenes zostericola* were found in the course of studies on the Queensland Gold Coast sea-grass fauna. The earlier collections of *P. zostericola* were in one case found in association with an anemone. Anemones are commonly found amongst sea grass meadows. Pontoniine shrimps with biunguiculate ambulatory dactyls are generally found in association with an invertebrate host. It seems possible that the collecting activities disturbed the shrimps from their host associations.

In *Phycomenes zostericola* the exopods of the maxillipeds are well developed but slender and feebly setose, with only 4 terminal plumose setae. This corresponds closely with the larval stages of many pontoniine shrimps, e.g., *Periclimenes brevicarpalis* (Schenkel 1902), described recently by Nagai & Shokita (2003). This should be considered as the plesiomorphic state of this character and is also found in species of the *Periclimenes obscurus* group such as *P. delagoae* Barnard (Bruce 1987). The other pontoniine genera with a well developed median process on the fourth thoracic sternite have well developed broader maxillipedal exopods that are generally provided with numerous long plumose setae distally and along distal medial and lateral margins, e.g. *Kemponia grandis* (Stimpson) (Bruce 1976, fig. 2).

Davie (2002) reports *P. zostericola* (as *Periclimenes indicus*) from 50 m, presumably a typographic error for 0.5 m. All records so far are from shallow waters, the deepest being only 2.0 m.

A collection of numerous carideans from shallow water sea grass beds from southern Western Australia (WAM C38246, from between Favorite Is. and Boullanger Island, 30°17'S, 115°00'E, 1.05.2005, M. Glenn & C.Whisson, box trawl) has been examined. No specimens of *P. zostericola* were found and the collection was dominated by hippolytid shrimps with only three species of palaemonid shrimps: *Leander manningi* Bruce, 2002, *Periclimenes aesopius* (Bate, 1853) and *Kemponia seychellensis* (Borradaile, 1915).

ACKNOWLEDGEMENTS
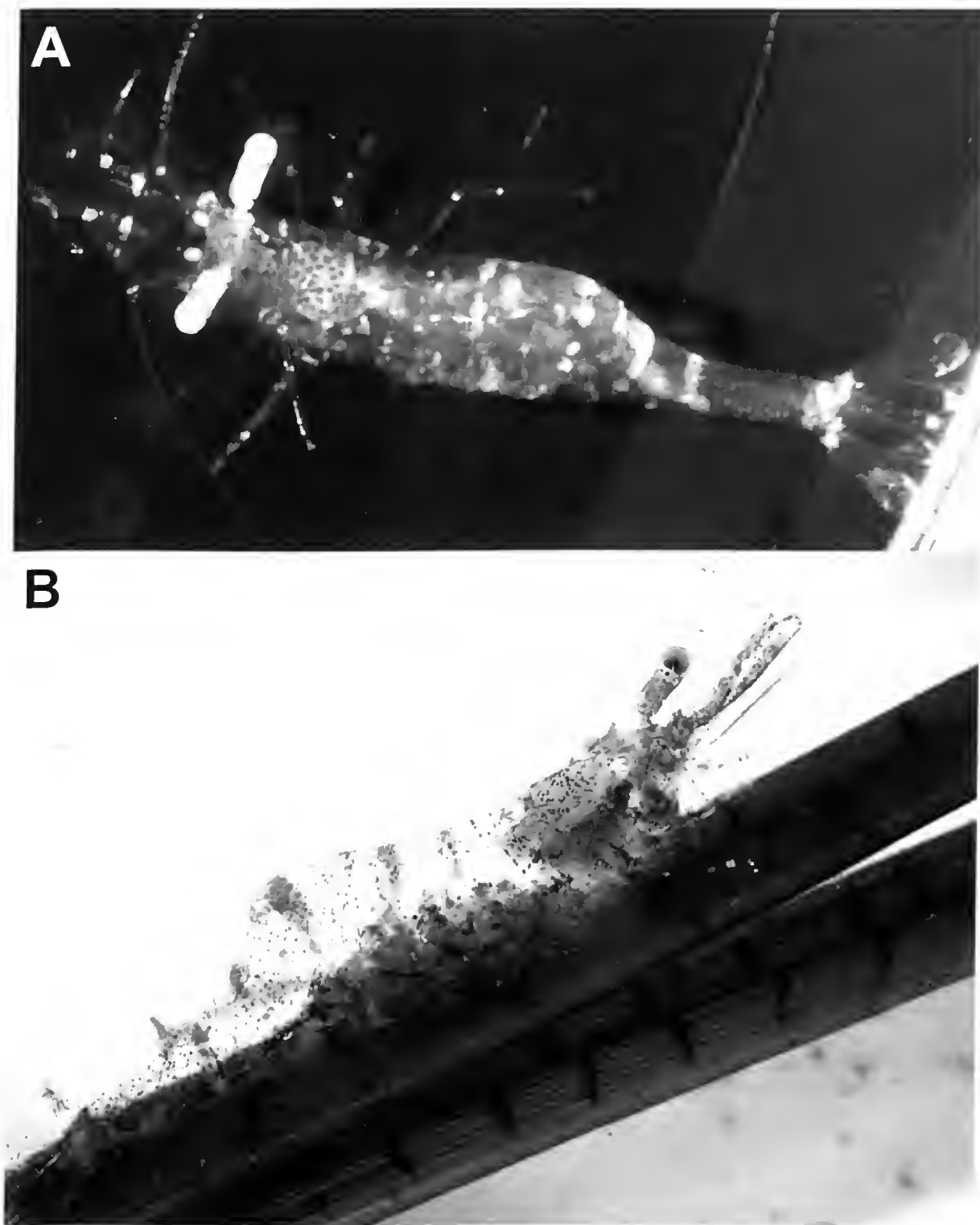
FIG. 7. *Phycomenes zostericola* gen. nov., sp. nov., Loder's Creek, SE Qld. **A**, dorsal aspect. **B**, lateral aspect (photos courtesy Jodie Haig).

the Northern Territory Museum collections and Melissa Titelius from the Western Australian Museum collections. Jodie Haig also kindly provided her photographs for use in this study. This study was also facilitated by support from the Australian Biological Resources Study.

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Palaemonid shrimps (Crustacea: Decapoda: Caridea) from Moreton Bay, Queensland, Australia

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ABSTRACT

Nineteen palaemonid species are reported from Moreton Bay, southeastern Queensland. These shrimps were mostly collected during the Thirteenth International Marine Biological Workshop — The Marine Fauna and Flora of Moreton Bay, Queensland. Nine species have not been previously recorded from Moreton Bay. Coloured photographs of living specimens are included. A key to all palaemonid shrimp species found from Moreton Bay is provided. ❑ *Crustacea; Decapoda; Palaemonidae; taxonomy; Moreton Bay; Queensland; Australia; new records.*

The palaemonid fauna of Moreton Bay, Queensland, has been reported or noted previously by Patton (1966), some papers by Bruce (Bruce 1977a, 1981a, b, 1988, 1998; Bruce & Coombes 1995, 1997) and by Davie (1998, 2002). With the results of the present study, there are now 39 species known from the Bay, including five species of the subfamily Palaemoninae and 34 species of the subfamily Pontoniinae (see Table 1). Of the collection of 19 species reported on here, nine are recorded from this area for the first time (see Table 1).

The present material was all collected as part of The Thirteenth International Marine Biological Workshop — The Marine Fauna and Flora of Moreton Bay, Queensland, held from 7–25 February 2005. All examined material is deposited in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China (IOCAS). Synonymies are restricted to significant works, and previous reports from Moreton Bay and the coast of Queensland. Species are listed in alphabetical order within subfamilies.

Previous records of two species, *Periclimenes indicus* and *P.* nr *obscurus*, by Bruce (1977b) and Wadley (1978) respectively, have now both been attributed to a new species and new genus, *Phycomenes zostericola* Bruce, 2008 (this vol.). A key to all 39 species known from Moreton Bay is provided later in the paper.

Rostral dentition is given in the form of a formula, e.g. '1+4-6/1-3', means 1 rostral tooth placed on the carapace behind the orbit, 4–6 other dorsal teeth, and 1–3 ventral teeth.

SYSTEMATIC ACCOUNT

PALAEMONINAE Rafinesque, 1815

Palaemon serenus (Heller, 1862)
(Fig. 1)

Leander serenus Heller, 1862: 527 (type locality: Sydney, Australia); 1865: 110, pl. 10, fig. 5; Hale, 1924: 68; 1927: 59, fig. 54; Kemp, 1925: 292.
Palaemon serenus — Holthuis, 1952a: 204; Wadley, 1978: 19, fig. 9g; Davie, 1998: 146, unnumbered colour photo; 2002: 300.

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, 5♀♀, Myora (27°28.092'S, 153°25.323'E), intertidal zone, seagrass bottom, J. Markham, 14.02.2005; IOCAS, 58 specimens, intertidal zone, rocky shore, in pools or holes, Dunwich, X. Li, 19.02.2005.

Distribution. Eastern and South Australia; littoral to sublittoral. Previously reported from Moreton Bay by Davie (1998).

Table 1. Species list of Palaemonidae found from Moreton Bay (* = first confirmed record from Moreton Bay).

	Species	Author
1	*Macrobrachium intermedium* (Stimpson, 1860)	Wadley (1978); Young & Wadley (1979)
2	*Macrobrachium novaehollandiae* (De Man, 1908)	Davie (1998); Short (2004)
3	*Palaemon debilis* Dana, 1852	Wadley (1978) ; Young & Wadley (1979)
4	*Palaemon serenus* (Heller, 1862)	Wadley (1978); Young & Wadley (1979); Davie (1998); **present**
5	*Palaemon serrifer* (Stimpson, 1860)	Davie (1998)
6	*Anchistus custos* (Forskål, 1775)	Davie (1998); **present**
7	*Apopontonia dubia* Bruce, 1981	Bruce (1981a)
8	*Conchodytes meleagrinae* Peters, 1852*	**present**
9	*Coralliocaris graminea* (Dana, 1852)	Patton (1966)
10	*Coralliocaris superba* (Dana, 1852)	Patton (1966)
11	*Harpiliopsis beaupresii* (Audouin, 1825)*	**present**
12	*Jocaste lucina* (Nobili, 1901)	Patton (1966)
13	*Kemponia amymone* (De Man, 1902)	Patton (1966); **present**
14	*Kemponia anacanthus* (Bruce, 1988	Bruce (1988); **present**
15	*Kemponia andamanensis* (Kemp, 1922)	Wadley (1978); Young & Wadley (1979); present
16	*Kemponia calmani* (Tattersall, 1921)*	**present**
17	*Kemponia elegans* (Paulson, 1875)*	**present**
18	*Kemponia grandis* (Stimpson, 1860)*	**present**
19	*Kemponia tenuipes* (Borradaile, 1898)*	**present**
20	*Laomenes nudirostris* (Bruce, 1968)	Bruce (1971); **present**
21	*Onycocaris stradbrokei* Bruce, 1998	Bruce (1998)
22	*Palaemonella rotumana* (Borradaile, 1898)	Bruce (1970a)
23	*Palaemonella spinulata* Yokoya 1936	Bruce (1983)
24	*Periclimenaeus bidentatus* Bruce, 1970b	Bruce (1983); **present**
25	*Periclimenaeus hecate* (Nobili, 1904)*	**present**
26	*Periclimenaeus myora* Bruce, 1998	Bruce (1998)
27	*Periclimenaeus zanzibaricus* Bruce, 1969a	Bruce (2006)
28	*Periclimenes brevicarpalis* (Schenkel, 1902)	Davie (1998); **present**
29	*Periclimenes cobourgi* Bruce & Coombes, 1995*	**present**
30	*Periclimenes commensalis* Borradaile, 1915	(Bruce, 1971)
31	*Periclimenes holthuisi* Bruce, 1969b	Wadley (1978); Young & Wadley (1979); Davie (1998); **present**
32	*Periclimenes inornatus* Kemp, 1922	Patton (1966)
33	*Periclimenes ruber* Bruce, 1982	Bruce (1982)Bruce, 1982c
34	*Periclimenes sarkanae* Bruce, 2007	Bruce (2007); **present**
35	*Periclimenes soror* Nobili, 1904	Davie (1998)
36	*Periclimenes terangeri* Bruce, 1998	Bruce (1998)
37	*Phycomenes zostericola* Bruce, 2008	Bruce (1977b)(*'indicus'*); Wadley (1978), Young & Wadley (1979) ('nr *obscurus'*); Bruce, 2008
38	*Pontoniopsis comanthi* Borradaile, 1915*	**present**
39	*Tuleariocaris holthuisi* Hipeau-Jacquotte, 1965	Bruce (1990)

FIG. 1. *Palaemon serenus* (Heller, 1862), Myora anterior carapace and appendages showing colour striping patterns.

Remarks. The specimens were semi-transparent in life, with fine brownish red spots and oblique dark stripes on the body surface.

Subfamily PONTONIINAE Kingsley, 1878

Anchistus custos (Forsskål, 1775)
(Fig. 2)

Cancer custos Forsskål, 1775: 94 (type locality: Al Luhayyah, Yemen).
Pontonia inflata H. Milne Edwards, 1840: 633 (type locality: Sri Lanka and Vanikoro, Santa Cruz Is.).
Anchistia aurantiaca Dana, 1852: 25 (type locality: Fiji Islands); 1855: 12, pl. 38, fig. 2.
Harpilius inermis Miers, 1884: 291, pl. 32, fig. B (type locality: Port Molle, Queensland).
Pontonia pinnae Ortman, 1894: 16, pl. 1, fig. 3 (type locality: Tanzania).

Anchistus custos – Holthuis, 1952b: 105, figs 43, 44; Morton, 1987: 129, figs 1–3, 6–9; Chace & Bruce, 1993: 72; Bruce & Coombes, 1995: 106; Bruce, 1996: 205; Davie, 1998: 96, unnumbered colour photo; 2002: 305; De Grave, 1999: 129, fig. 3, pl. 1b–c; Li, 2000: 7, fig. 8; Li & Bruce, 2006: 625.

Material Examined: North Stradbroke I., Moreton Bay: IOCAS, 4 ♂♂, 4 ovig. ♀ (4 couples), 1 juv., Dunwich (27°29.642′S, 153°23.789′E), intertidal, with *Pinna bicolor*. X. Li and J. Markham, 9.02.2005; IOCAS, 3 ♂♂, 3 ovig. ♀♀, Dunwich (27°29.6′S, 153° 23.8′E), 1.6–2.4m, with *Pinna bicolor*, SCUBA, X. Li, 11.02.2005; IOCAS, ♂, Myora (27°28.092′S, 153° 25.323′E), intertidal, with *Pinna bicolor*, B. Morton, 13.02.2005; IOCAS, 3 ♂♂, 3 ovig. ♀♀, Amity Point (27°24.043′S, 153°28.260′E), 2–7.8m, associated with *Pinna bicolor*, ♀ parasitised by a bopyrid in branchial chamber. SCUBA, X. Li, 14.02.2005; IOCAS, ♂, ovig. ♀, Dunwich (27°29.6′S, 153°23.8′E), intertidal, with *Pinna bicolor*, Daphne

FIG. 2. *Anchistus custos* (Forsskål, 1775) **A**, Shag Rock, male/female pair, dorsal view; **B**, Dunwich, male/female pair, dorsal view; **C**, Amity Point, ovig. ♀, lateral view, showing parasite in branchial chamber.

Fautin, 14.02.2005; IOCAS, 3 ♂♂, 2 ovig. ♀♀, Amity Point (27°24.249′S, 153°26.215′E), 2–5m, associated with *Pinna bicolor*, SCUBA, X. Li, 15.02.2005; IOCAS, 4 ♂♂, 5 ovig. ♀♀, Henderson's Gutter (27°20.879′S, 153°24.715′E), 0.5–1.5m, seagrass bottom, associated with *Pinna bicolor*, snorkeling, X. Li, 17.02.2005; IOCAS, ♂, ovig. ♀, Shag Rock (27°24.855′S, 153°31.599′E), Point Lookout, 7–11m, with *Pinna bicolor*, SCUBA, X. Li, 18.02.2005; IOCAS, ♂, ♀, Shag Rock (27°24.855′S, 153°31.599′E), Point Lookout, 7–11m, with *Atrina (Atrina) vexillum*. X. Li, 18.02.2005; IOCAS, ♂, ovig. ♀, Shag Rock (27°24.476′S, 153°31.504′E), Point Lookout, 6–8m, with *Atrina (Atrina) vexillum*. SCUBA, X. Li, 21.02.2005.

Distribution. Known from Red Sea and eastern Africa to Philippines, southward to Australia (South Australia), and eastward to the Caroline Islands and Fiji; littoral to 20m depth. Previously reported from Moreton Bay by Davie (1998).

Remarks. Ovigerous females with more than 400 small eggs. Specimens were covered with dense fine red and white spots on the body.

Conchodytes meleagrinae Peters, 1852
(Fig. 3)

Conchodytes meleagrinae Peters, 1852: 594 (type locality: Mozambique); Bruce, 1977a: 73, fig. 14c, d; Chace & Bruce, 1993: 74; Li, 2000: 25, fig. 26; Davie, 2002: 307; Li & Bruce, 2006: 628.

Material Examined. ♂, ovig. ♀, Amity Point (27°24.249′S, 153°26.215′E), North Stradbroke I.,
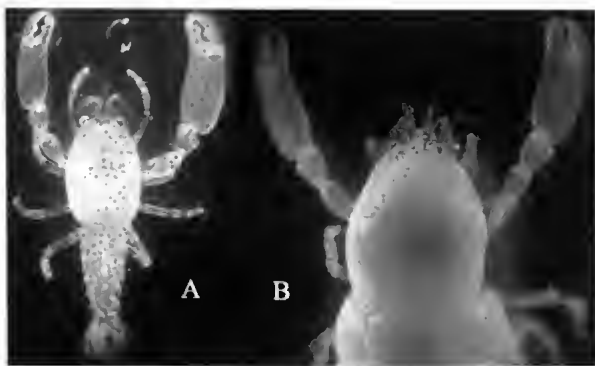
FIG. 3. *Conchodytes meleagrinae* Peters, 1852, Amity Point (27°24.249'S, 153°26.215'E), male/female pair, dorsal view.

FIG. 4. *Harpiliopsis beaupresii* (Audouin, 1825), Shag Rock, ovig. ♀, dorsal view.

Moreton Bay, 2–5m, associated with oyster, *Pinctada margritifera*, SCUBA, X. Li, 15.02.2005.

Distribution. Australia (Great Barrier Reef, northeast Qld, NT, WA); widely distributed in Indo-Pacific Red Sea east to Hawaii; littoral to sublittoral. Not previously from Moreton Bay.

Remarks. Specimens were transparent to semi-transparent; body and appendages covered with red and white spots; ovigerous female with more numerous white spots than the male. Ovigerous female with more than 200 eggs.

Harpiliopsis beaupresii (Audouin, 1825)
(Fig. 4)

Palaemon Beaupresii Audouin, 1825: 91 (type locality: Egyptian Red Sea); 1827: 276, pl. 10, fig. 4.
Harpiliopsis beaupresi — Borradaile, 1917: 324, 379, pl. 55, fig. 21; Holthuis, 1952b: 181, fig. 89.
Harpiliopsis beaupresii — Patton, 1966: 276; Bruce, 1976: 124, figs 21, 22; Bruce & Coombes, 1995: 109; Li, 2000: 61, fig. 65; Davie, 2002: 312; Li & Bruce, 2006: 635.

Material Examined. ♂, ovig. ♀, Shag Rock (27°24.476'S, 153°31.504'E), Point Lookout, North Stradbroke I., 6–8m, with *Seriotopora* sp., SCUBA, X. Li, 21.02.2005.

Distribution. Australia (WA, NT, Qld); widely distributed in the Indo-Pacific from Red Sea, and Madagascar, to Hawaii and Easter I.. Not previously from Moreton Bay.

Remarks. Littoral to sublittoral. Body was semi-transparent, slight greenish, with longitudinal dark-red fine stripes; eyestalks and legs with dark-red spots.

Kempouia amymoue (De Man, 1902)
(Fig. 5A)

Periclimenes amymoue De Man, 1902: 829–833, pl. 25 fig. 53 (type locality: Ternate, Indonesia); Bruce, 1977a: 43; 1991: 235; Bruce & Coombes, 1995: 123; Li, 2000: 155, fig. 190; Davie, 2002: 323.
Periclimenes (*Harpilius*) *amymoue* — Holthuis, 1952b: 82, fig. 32; Patton, 1966: 273.
Kempouia amymoue — Bruce, 2004: 11; Li & Bruce, 2006: 641.

Material Examined. 4 ♂♂, 2 ovig. ♀♀, Shag Rock (27°24.476'S, 153°31.504'E), Point Lookout, North Stradbroke I., 6–8m, dead or living (*Seriotopora* sp.) corals, and anemone *Heteractis crispa*, SCUBA, X. Li, 21.02.2005.

Distribution. Australia (northwest coast, WA; NT; Great Barrier Reef, northeast coast, Qld); Red Sea, Andaman Islands, New Caledonia, Solomon Islands, Philippines, Marshall Islands,
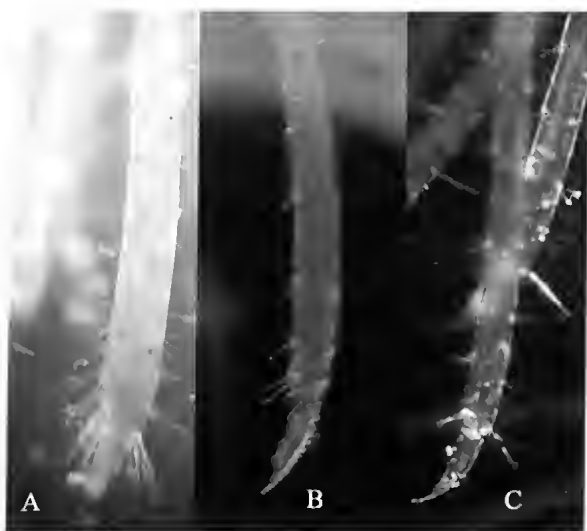
FIG. 5. Propodus and dactylus, ambulatory pereiopod. **A**, *Kemponia amymone* (De Man, 1902), Shag Rock; **B**, *K. elegans* (Paulson, 1875), Shag Rock; **C**, *K. grandis* (Stimpson, 1860), Shag Rock.

Nicobar Islands; littoral to sublittoral. Previously reported from Moreton Bay by Patton (1966).

Remarks. Specimens were transparent, covered with sparse red spots on the body and appendages. The propodus of the ambulatory pereiopods has long setae along the ventral surface, and is without spines.

Kemponia anacanthus (Bruce, 1988)

Periclimenes anacanthus Bruce, 1988: 105, figs 1-5 (type locality: Polka Point, Moreton Bay, Australia); Bruce & Coombes, 1995: 125, fig. 12a; Li, 2000: 156, fig. 191; Davie, 2002: 323.
Kemponia anacanthus — Bruce, 2004: 12; Li & Bruce, 2006: 641.

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, ♀♀ (1 ovig.), Dunwich, intertidal, with *Cladiella* sp., X. Li, 11.02.2005; IOCAS, ♂, Dunwich, intertidal, seagrass bottom, X. Li, 11.02.2005; IOCAS, ♂, Dunwich, intertidal, with *Cladiella* sp., X. Li, 12.02.2005; IOCAS, ovig. ♀, Dunwich, intertidal, with sea algae. X. Li, 15.02.2005; IOCAS, 2 ♀♀, Dunwich, intertidal, with red algae, *Acanthophora spicifera*. X. Li, 15.02.2005; IOCAS, 1 juv., Shag Rock (27°24.855'S, 153°31.599'E), Point Lookout, 7–11m, coral reef. SCUBA, X. Li, 18.02.2005.

Distribution. Australia (northern coast of NT; central east Qld). Previously recorded from Moreton Bay by Bruce (1988).

FIG. 6. *Kemponia andamanensis* (Kemp, 1922), Myora, intertidal zone, algae, ovig. ♀, dosal view.

Remarks. The specimens were transparent, with sparse fine red spots underneath the body surface. The second pereiopods, the sixth abdominal somite, and the telson were white. The male specimens with the body, rostrum and pereiopods are distinctly more slender and longer than those of females.

Kemponia andamanensis (Kemp, 1922)
(Fig. 6)

Periclimenes (Ancylocaris) andamanensis Kemp, 1922: 204, figs 54-57 (type locality: Ross Channel, Andamans).
Periclimenes (Harpilius) andamanensis — Holthuis, 1952b: 79.
Periclimenes andamanensis — Bruce, 1977c: 269; Li, 2000: 156, fig. 192; Davie, 2002: 323.

Periclimenes (*Harpilius*) nr *andamanensis* — Wadley, 1978: 19, fig. 9i.
Kemponia andamanensis — Bruce, 2004: 12; Li & Bruce, 2006: 642.
Kemponia cf. *andamanensis* — Li *et al.*, 2004: 529, fig. 16.
Material Examined. North Stradbroke I., Moreton Bay: IOCAS, 19 ♂♂, 12 ♀♀ (4 ovig.), Myora (27°28.092'S,153°25.323'E), intertidal zone, seagrass bottom, X. Li, 12.02.2005; IOCAS, 40 specimens (15 ovig. ♀♀), Myora (27°28.092'S, 153°25.323'E), intertidal zone, seagrass bottom, J. Markham, 14.02.2005; IOCAS, 6 ♂♂, Adam's Beach, Dunwich, intertidal zone, seagrass *Zostera copricaorni*, X. Li, 16.02.2005; IOCAS, 17 ♂♂, 8 ovig. ♀♀, Amity Point, intertidal zone, seagrass bottom, X. Li, 20.02.2005; IOCAS, 8 ♂♂, 11 ovig. ♀♀, Myora (27°28.115'S, 153°25.228'E), intertidal zone, seagrass bottom, J. Markham, 20.02.2005; IOCAS, ovig. ♀, Myora, intertidal zone, algae, A. Crowther, 20.02.2005.

Distribution. Australia (northeast Qld); Indo-West Pacific; 7–15 m. Previously recorded from Moreton Bay by Wadley (1978).

Remarks. Specimens were transparent, with fine sparse yellowish spots on the dorsal surface, and reddish spots beneath the surface of the body. The distal part of the palm and proximal part of the fingers of the second pereiopod were yellow. Merus-carpus and carpus-chela are white yellow. Tail-fan has big white spots. Second pereiopods of males are distinctly more slender and longer than those of females.

Kemponia calmani (Tattersall, 1921)

Periclimenes calmani Tattersall, 1921: 385, pl. 27, fig. 11, pl. 28, figs 14–15 (type locality: Sudan coast, Red Sea); Bruce, 1987: 1415, figs 1–5; Li, 2000: 165, fig. 204.
Periclimenes (*Ancylocaris*) *calmani* — Kemp, 1922: 176.
Kemponia calmani — Bruce, 2004: 13.
Material Examined. 2 ♂♂, Dunwich, North Stradbroke I., Moreton Bay, intertidal, with *Cladiella* sp., X. Li, 12.02.2005.
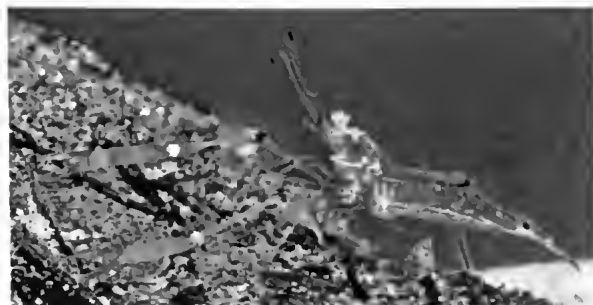
FIG. 7. *Kemponia tenuipes* (Borradaile, 1898) at Amity Point, North Stradbroke Is. (Photo courtesy Rudi Kuiter).

Distribution. Australia (Qld); Egypt, Sudan, Malaya, Indonesia, eastern Mediterranean. Not previously recorded from Australian waters.
Remarks. Specimens were transparent in life.

Kemponia elegans (Paulson, 1875)
(Fig. 5B)

Anchistia elegans Paulson, 1875: 113, pl. 17, fig. 1 (type locality: Red Sea).
Periclimenes (*Falciger*) *dubius* Borradaile, 1915: 211 (type locality: Laccadive Islands).
Periclimenes elegans — Bruce, 1977a: 42; 1983: 884, 898; Chace & Bruce, 1993: 110; Bruce & Coombes, 1995: 129; Li, 2000: 178, fig. 225; Davie, 2002: 326.
Kemponia elegans — Bruce, 2004: 14; Li & Bruce, 2006: 643.
Material Examined. 2 ♂♂, 3 ♀♀ (2 ovig.), 2 juvs, Shag Rock (27°24.476'S, 153°31.504'E), Point Lookout, North Stradbroke I., Moreton Bay, 6–8 m, dead or living (*Seriotopora* sp.) corals, and anemone *Heteractis crispa*, SCUBA, X. Li, 21.02.2005.

Distribution. Australia (WA, northern coast of NT, Great Barrier Reef and northeast coast of Qld); Indo-west Pacific from the Red Sea and western Indian Ocean to the Marshall Islands and Hawaiian Islands; intertidal to 53 m depth. Not previously recorded from Moreton Bay.
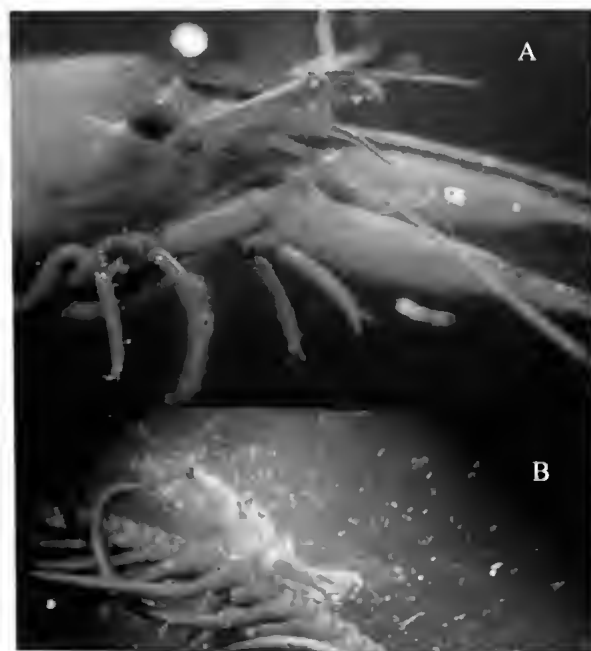
FIG. 8. *Laomenes nudirostris* (Bruce, 1968), Amity Point, ♂: A, anterior part of carapace and appendages, lateral view; B, with its host featherstar *Cenolia* sp.

Remarks. Specimens were transparent in life. The carapace and the merus of the second pereiopods are characterised by declining red stripes. The chela, carpus and merus of the second pereiopods have even fine brownish tubercles, with dark brownish encircles.

Kemponia grandis (Stimpson, 1860)
(Fig. 5C)

Anchistia grandis Stimpson, 1860: 39 (type locality: Ryukyu Islands).
Periclimenes vitiensis Borradaile, 1898: 383 (type locality: Viti Levu, Fiji Islands).
Periclimenes grandis — Borradaile, 1898: 382; Bruce, 1977a: 42; Chace & Bruce, 1993: 112; Li, 2000: 186, fig. 235; Davie, 2002: 327.
Kemponia grandis — Bruce, 2004: 16; Li *et al.* 2004: 530; Li & Bruce, 2006: 644.

Material Examined. 2 ♂♂, ♀, Shag Rock (27°24.476′S, 153°31.504′E), Point Lookout, North Stradbroke I., Moreton Bay, 6–8 m, with anemone *Heteractis crispa*, SCUBA, X. Li, 21.02.2005.

Distribution. Australia (NT, Qld); widespread in Indo-West Pacific from the Red Sea and east coast of Africa to French Polynesia. Not previously recorded from Moreton Bay.

Remarks. Live specimens were transparent; palm, carpus and merus of second pereiopods have a red circled stripe respectively.

Kemponia tenuipes (Borradaile, 1898)
(Fig. 7)

Periclimenes tenuipes Borradaile, 1898: 384 (type locality: New British); Bruce & Coombes, 1995: 135; Li, 2000: 240, fig. 319; Davie, 2002: 322.
Periclimenes borradailei Rathbun, 1904: 34 (unnecessary nom. nov. for *Periclimenes tenuipes* Borradaile, 1898).
Periclimenes (*Falciger*) *borradailei* — Borradaile, 1917: 324, 372.
Periclimenes (*Ancylocaris*) *tenuipes* — Kemp, 1922: 220, pl. 8, fig. 11.
Periclimenes (*Harpilius*) *tenuipes* — Holthuis, 1952b: 84.
Kemponia tenuipes — Bruce, 2004: 19.

Distribution. Australia (NT, Qld); Indo-West Pacific from East Africa and Red Sea to New Caledonia, Marshall Islands, and Fiji. Not previously recorded from Moreton Bay.

Remarks. This record is based on a photo (Fig. 7) taken at Amity Point, North Stradbroke I., in September 1986 by Rudi Kuiter, and used with his kind permission. Unfortunately the specimen was not collected. The photo shows that this species is transparent in life; the second pereiopods have orange fingers; bright yellowish to green or orange strips found on eyes, anterior carapace, tail-fan, and distal carpus of second pereiopods; and black circle or stripe on distal meri of second and first pereiopods, distal scaphocerite, distal pleuron of sixth abdominal somite and dorsomedian tergum of third abdominal somite. A second photo shows rostral dentition to be 10/5, possibly 10/6 (A.J. Bruce, pers. comm.).

Laomenes nudirostris (Bruce, 1968)
(Fig. 8)

Parapontonia nudirostris Bruce, 1968: 1149, figs 1–5 (type locality: Nouméa, New Caledonia); 1981b: 9; 1992: 78, figs 25–27; Li, 2000: 114, fig. 125; Davie, 2002: 318.
Laomenes nudirostris — Okuno & Fujita, 2007: 121, fig. 3.

Material Examined. ♂, Amity Point (27°24.249′S, 153°26.215′E), North Stradbroke I., Moreton Bay, 2–5m, associated with featherstar *Cenolia* sp., SCUBA, X. Li, 15.02.2005.

Distribution. Australia (Qld); New Caledonia; Papua New Guinea?; Japan; Kume I.; Okinawa. First recorded from North Stradbroke I. by Bruce (1981b).

Remarks. The specimen agrees well with the descriptions and illustrations of Bruce (1968, 1992), except that the dactylus of the ambulatory pereiopods all lack the accessory tooth. On the host featherstar, there was one male and one ovigerous female living on the same host (the female escaped). The body is dark red, similar to its host. After preservation in alcohol for more than one and a half years, the colour still remains dark.

Periclimenaeus bidentatus Bruce, 1970

Periclimenaeus bidentatus Bruce, 1970b: 305 (type locality: Heron I., Queensland); 1991: 254, fig. 18; Li, 2000: 119, fig. 131; Davie, 2002: 319.

Material Examined. 2 ♀♀, Dunwich (27°29.642′S, 153°23.789′E), North Stradbroke I., Moreton Bay, intertidal, with sponge, X. Li, 9.02.2005.

Distribution. Australia (northern coast NT, east coast of Qld, Great Barrier Reef, Hibernia Reef, WA); New Caledonia, Papua New Guinea and Zanzibar. Previously recorded from Moreton Bay by Bruce (1983).

Remarks. Specimens were transparent in life; appendages have red stripes, and the rostral formula is 6/0.

Periclimenaeus hecate (Nobili, 1904)

Coralliocaris hecate Nobili, 1904: 232 (type locality: Djibouti).

Periclimenaeus hecate — Balss, 1921: 14; Bruce, 1974: 1574, figs 11, 12, 13E; 2002: 577, fig. 8; Li, 2000: 124, fig. 143; Davie, 2002: 320.

Material Examined. IOCAS, ♂, Shag Rock (27° 24.855'S, 153°31.599'E), Point Lookout, North Stradbroke I., Moreton Bay, coral reef, 7–11 m, SCUBA, X. Li, 18.02.2005.

Distribution. Australia (northeast coast Qld, Great Barrier Reef, northwest coast of WA); many localities of Indo-West Pacific. Not previously recorded from Moreton Bay.

Remarks. Specimen was transparent in life. The rostral formula is 4/0.

Periclimenes brevicarpalis (Schenkel, 1902)
(Fig. 9)

Periclimenes amboinensis Zehntner, 1894: 206, pl. 9, fig. 27 (non *Periclimenes amboinensis* de Man, 1888).

Ancylocaris brevicarpalis Schenkel, 1902: 563, pl. 13, fig. 21 (type locality: Amboina, Indonesia).

Palaemonella aberrans Nobili, 1904: 234 (type locality: Djibouti).

Harpilius latirostris Lenz, 1905: 380, pl. 47, fig. 14–14b (type locality: Zanzibar).

Periclimenes potina Nobili, 1905: 159 (type locality: southeast coast of Arabia).

Periclimenes hermitensis Rathbun, 1914: 655, pl. 1, figs 1–3 (type locality: Monte Bello I.).

Periclimenes (Ancylocaris) brevicarpalis — Kemp, 1922: 185–191, figs 40–42, pls 67.

Periclimenes (Harpilius) brevicarpalis — Holthuis, 1952b: 69–73, fig. 27.

Periclimenes brevicarpalis — Bruce, 1991: 236; Chace & Bruce, 1993: 104; Bruce & Coombes, 1995: 125; Davie, 1998: 211, unnumbered colour photo; 2002: 324; Li, 2000: 161, fig. 199; Li & Bruce, 2006: 676.

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, 2 ♂♂, Dunwich (27°29.6'S, 153° 23.8'E), intertidal, with anemone *Stichodactyla haddoni*, X. Li, 11.02.2005; IOCAS, 3 ♂♂, ovig. ♀, Henderson's Gutter (27°20.879'S, 153°24.715'E), 0.5–1.5 m, seagrass bottom, associated with anemone *Stichodactyla haddoni*, snorkeling, X. Li, 17.02.2005.

Distribution. Australia (northern coast of NT, Great Barrier Reef and northeast coast of Qld); widespread in Indo-west central Pacific. Previously recorded from Moreton Bay by Davie (1998).

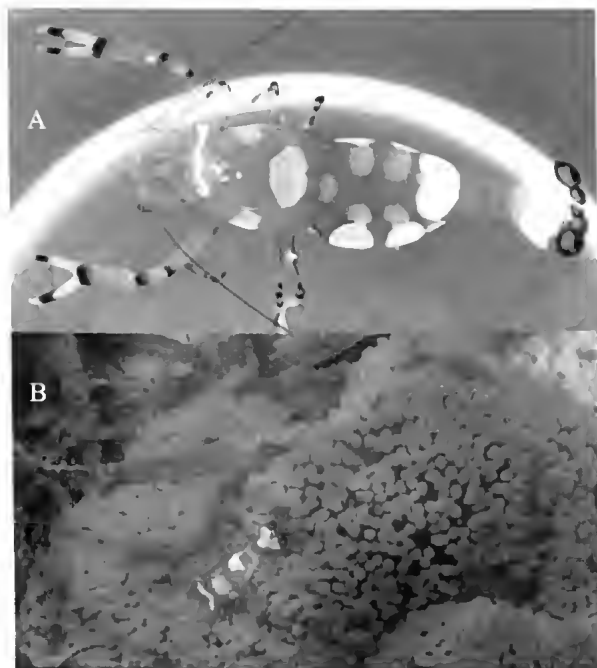FIG. 9. *Periclimenes brevicarpalis* (Schenkel, 1902). **A**, Dunwich, ovig. ♀, dosal view; **B**, Henderson's Gutter, ovig. ♀, shows association with host anemone *Stichodactyla haddoni*.
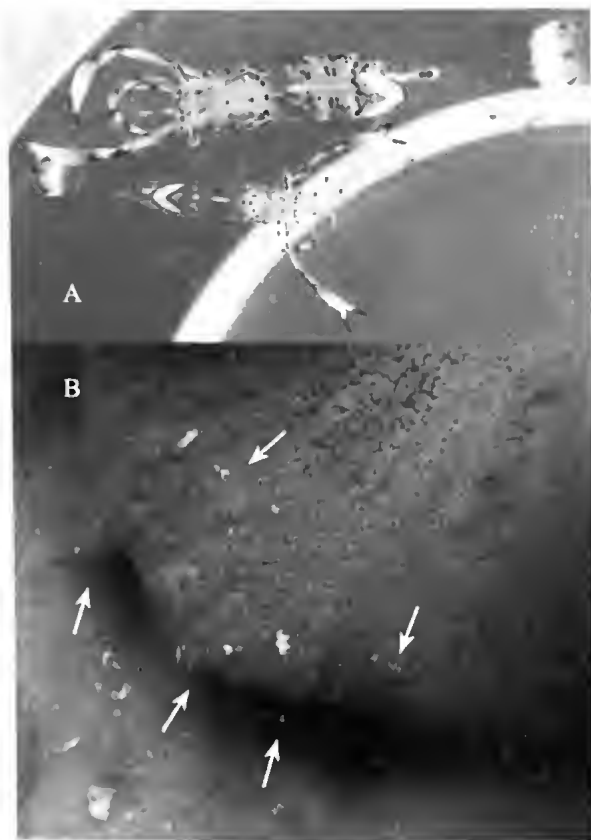
FIG. 10. *Periclimenes holthuisi* Bruce, 1969. **A**, Dunwich, male/femal pair in dorsal view; **B**, Dunwich, intertidal, 12.02.2005, group of the shrimps showing the association with host anemone *Stichodactyla haddoni*.
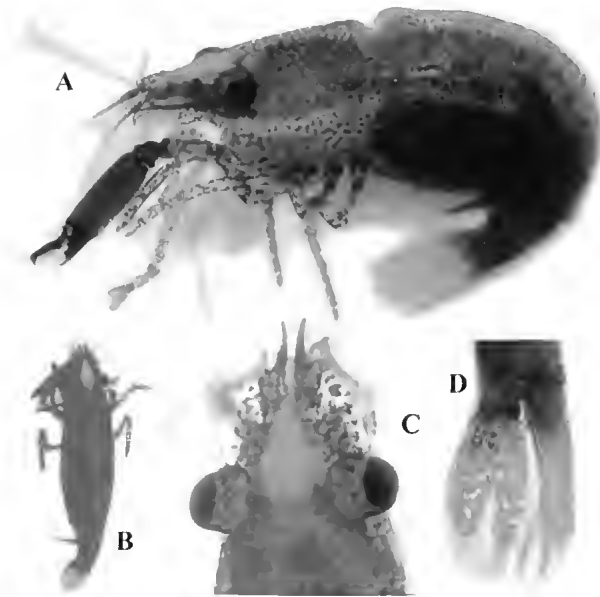
FIG. 11. *Pontoniopsis comanthi* Borradaile, 1915, Shag Rock, ovig. ♀. **A**, body, lateral view; **B**, body, low magnification, dorsal view; **C**, anterior part of carapace, dorsal view; **D**, tailfan, lateral view.

Periclimenes cobourgi Bruce & Coombes, 1995

Periclimenes cobourgi Bruce & Coombes, 1995: 125, figs 10–11 (type locality: Cobourg Peninsula, NT, Australia); Li, 2000: 168, fig. 207; Davie, 2002: 325.

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, 4 ♀♀ (2 ovig.), Dunwich, intertidal seagrass, X. Li, 11.02.2005; IOCAS, ovig. ♀, Dunwich, intertidal seagrass, with *Cladiella* sp. [Alcyonacea], X. Li, 12.02.2005; IOCAS, 248 specs (72 ovig. ♀♀), Myora (27°28.092'S, 153°25.323'E), intertidal zone, seagrass, X. Li, 12.02.2005; IOCAS, ♂, 11 ♀♀ (10 ovig.), Myora (27°28.092'S, 153°25.323'E), intertidal zone, seagrass, J. Markham, 14.02.2005; IOCAS, 4 ♂♂, 8 ♀♀ (4 ovig.), Adam's Beach, Dunwich, intertidal zone, seagrass *Zostera capricorni*, X. Li, 16.02.2005; IOCAS, 101 specs (46 ovig. ♀♀), Amity Point, intertidal, seagrass, X. Li, 20.02.2005.

Distribution. Previously recorded from the type locality, Cobourg Peninsula, NT, Australia. This is the second record for the species.

Remarks. The peculiar stout anterior median process on the fourth sternite of these specimens is typical of both *Periclimenes indicus* (Kemp, 1915) and *Periclimenes cobourgi* Bruce & Coombes, 1995. The following characters agree more closely with *P. cobourgi*: 1) rostral dentition 1 + 5–6 (mostly 6)/0–2 (mostly 2, rarely 0); 2) rostrum reaches or overreaches distal end of

antennule peduncle; with dorsal margin usually slightly convex; 3) epigastric spine located at about anterior 0.3 of carapace length; 4) hepatic spine located in high, anterior position; 5) antero-lateral angle of branchiostegite usually bluntly obtuse, not protruding; 6) eye stalk c. 0.4 of carapace length, reaching to about proximal 0.4 of rostrum; 7) corneal diameter c. 0.22 of carapace length, 0.6 of stalk length; 8) accessory pigment spot on feebly raised tubercle; 9) upper flagellum of antennule with proximal 7–8 segments fused; shorter ramus includes 2–3 segments; scaphocerite slightly exceeds antennular peduncle; 10) ambulatory pereiopod with long ventral spines on distal half of propodus; 11) spines are more or less as long as the propodus depth;12) distoventral pair of spines are usually less than and sometimes as long as half the dactylar length; 13) dactylus with accessory tooth is usually longer than half the unguis; 14) telson with posterior margin has a small acute median process.

Periclimenes holthuisi Bruce, 1969
(Fig. 10)

Urocaris longicaudata Pearson, 1905: 78, pls 1, fig. 5. (non *U. longicaudatus* Stimpson, 1860)
Periclimenes (*Periclimenes*) *aesopius* Holthuis, 1952b: 34, figs 5, 6. (non *Anchistia aesopia* Bate, 1863)
Periclimenes holthuisi Bruce, 1969b: 258 (type locality: Hong Kong); Chace & Bruce, 1993: 113; Bruce & Coombes, 1995: 130; Davie, 1998: 97, unnumbered colour photo; 2002: 327; Li, 2000: 190, fig. 241.
Periclimenes (*Periclimenes*) *holthuisi* — Wadley, 1978: 19, fig. 9j.

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, ♂, ♀, Dunwich, intertidal, with anemone *Stichodactyla haddoni*, X. Li, 9.02.2005; IOCAS, 6 ♂♂, 9 ♀♀ (2 ovig.), Dunwich (27°29.6'S, 153°23.8'E), intertidal, with anemone *Stichodactyla haddoni*, X. Li, 11.02.2005; IOCAS, 3 ♀♀, Dunwich, intertidal, with anemone *Stichodactyla haddoni*, X. Li, 12.02.2005; IOCAS, ♂, ♀, Henderson's Gutter (27°20.879'S, 153°24.715'E), 0.5–1.5 m, seagrass bottom, associated with anemone *Stichodactyla haddoni*, snorkeling, X. Li, 17.02.2005.

Distribution. Australia (northern coast of NT, Great Barrier Reef, east coast Qld); Indo-West Pacific from eastern Africa to Japan, New Caledonian and Marshall Islands. Previously recorded from Moreton Bay by Davie (1998).

Remarks. This species usually occurs in small groups associated with its host — this is in contrast with *Periclimenes brevicarpalis*, that is only ever found living as a heterosexual pair on its host anemone.

Periclimenes sarkanae Bruce, 2007

Periclimenes sarkanae Bruce, 2007: 61, figs 1–5 (type locality: Fisherman I., Moreton Bay, Australia).

Material Examined. North Stradbroke I., Moreton Bay: IOCAS, 11 ♂♂, 4 ♀♀ (3 ovig.), Dunwich, intertidal, with *Cladiella* sp., X. Li, 11.02.2005; IOCAS, ♀, Dunwich, intertidal, seagrass bottom, X. Li, 11.02.2005; IOCAS, 3 ♂♂, 4 ♀♀ (2 ovig.), Dunwich, intertidal, with anemone *Stichodactyla haddoni*, X. Li, 11.02.2005; IOCAS, 6 ♂♂, 11 ♀♀ (4 ovig.), Dunwich, intertidal, with *Cladiella* sp., X. Li, 12.02.2005; IOCAS, ovig. ♀, Dunwich, intertidal, with anemone *Stichodactyla haddoni*, X. Li, 12.02.2005; IOCAS, ovig. ♀, Dunwich, intertidal, with algae, X. Li, 15.02.2005.

Distribution. Only known from the type locality, Moreton Bay.

Remarks. The specimens agree well with the original description and illustrations of Bruce (2007). They were transparent in life, with small red spots on base of legs, and more or less on the body surface.

Pontoniopsis comanthi Borradaile, 1915
(Fig. 11)

Pontoniopsis comanthi Borradaile, 1915: 213 (type locality: Torres Strait); 1917: 377, pl. 57, fig. 27; Holthuis, 1952b: 153, figs 70, 71; Bruce, 1981c: 396, figs 3d, 4, 5; Li, 2000: 276, fig. 369; Davie, 2002: 337.

Material Examined. North Stradbroke I., Moreton Bay: ovig. ♀, Shag Rock (27°24.855′S, 153°31.599′E), Point Lookout, 7–11m, coral reef, associated with featherstar *Cenolia* sp., SCUBA, X. Li, 18.02.2005.

Distribution. Australia (northeast coast of Qld, Tasman Sea); Indo-West Pacific from Red Sea to Japan and Kiribati. Not previously recorded from Moreton Bay.

Remarks. In life the body was covered with dense dark red spots and stripes; the rostrum, tail-fan, dactylus of ambulatory pereiopods, and the distal part of the antennules are covered with sparse big orange yellow spots. Its colour pattern is similar to its host.

KEY TO THE PALAEMONIDAE OF MORETON BAY

1. Posterior margin of telson with two pairs of spines and one or more pairs of setae; base of third maxilliped with pleurobranch; mandible with three-segmented palp; carapace with branchiostegal suture; fourth thoracic sternite with distinct median process between first pereiopods; dactylus of ambulatory pereio-pods simple; rostrum straight, without elevated basal crest. Palaemoninae 2
— Posterior margin of telson with three pairs of posterior spines; base of third maxilliped without pleurobranch. Pontoniinae . . . 6

2. Carapace with hepatic spine, without branchiostegal spine; distal part of posterior margin of propodus of fifth pereiopod with numerous transverse rows of setae; second pereiopod with carpus longer than merus, fingers without row of enlarged tubercles at inner side of cutting edge, with at most one or two teeth on proximal part of cutting edge, rest of cutting edge entire . . . . *Macrobrachium* 3
— Carapace without hepatic spine, but with branchiostegal spine. *Palaemon* 4

3. Second pereiopod with fingers two fifths as long as palm. . . . . *Macrobrachium novaehollandiae* (De Man, 1908)
— Second pereiopod with fingers three quarters as long as palm. . . . . *Macrobrachium intermedium* (Stimpson, 1860)

4. Second pereiopod with carpus less than twice, longer than 1.5 times as long as chela; dorsal rostral teeth discontinuous, distal half entire except for subapical tooth; upper antennular flagellum with fused part subequal to, or longer than, free part of shorter ramus; scaphocerite at least as long as carapace; first pleopod of male with margin of endopod entire, without appendix. R: 1+1–7+1/3–10. . . . . *Palaemon debilis* Dana, 1852
— Second pereiopod with carpus shorter than chela; branchiostegal spine inserted on margin of carapace. 5

5. Upper antennular flagellum with fused part less than half as long as free part of shorter ramus, shorter ramus subequal to antennular peduncle; second pereiopod with carpus more than two-thirds as long as chela; rostrum deep, much expanded at level of first ventral tooth, with less than seven ventral teeth. R: 2–3+9–13/2–5. . . . . *Palaemon serrifer* (Stimpson, 1860)
— Upper antennular flagellum with fused part more than half as long as free part of shorter ramus; second pereiopod with fingers much longer than half as long as palm, carpus shorter than chela; only one tooth of dorsal rostral series situated on carapace posterior to level of orbital margin; basal

antennular segment with distolateral spine not overreaching adjacent convex distal margin. R: 2–3 + 6–9/3–4. . . . .
. . . . . . *Palaemon serenus* (Heller, 1862)

6. Mandible with palp; carapace with hepatic spine; transverse ridge on fifth thoracic sternite usually with pair of long, slender, acute submedian processes; second pereiopod with merus armed with sharp distoventral tooth. *Palaemonella* 7

— Mandible without palp; carapace with or without hepatic spine; transverse ridge on fifth thoracic sternite, if present at all, without pair of long, slender, acute submedian processes; second pereiopod with merus usually unarmed distoventrally; all maxillipeds provided with exopods. 8

7. Carapace with supraorbital spine; second pereiopod with ischium distoventrally unarmed; rostrum 0.9 times as long as carapace, exceeding end of third segment of antennular peduncle. R: 2+5/2 . . . .
. . . . . *Palaemonella spinulata* Yokoya, 1936

— Carapace without supraorbital spine, usually with supraorbital tubercle; second pereiopod with carpus armed distally with one or two marginal teeth; dactylus of ambulatory stout, no longer than six times basal depth; third pereiopod with flexor margin of dactylus regularly concave, not sinuous, distoventral propodal spines long.
. . *Palaemonella rotumana* (Borradaile, 1898)

8. Carapace with hepatic spine. 9
— Carapace without hepatic spine, without postorbital spines. 29

9. Epistome with a pair of horns; rostral lateral carina forming well developed supraorbital eaves, supraorbital tooth present; eye with cornea more or less produced distally as a papilla-like project (ogival); mandible with incisor process widened and multidentate; rstrum unarmed dorsally. *Laomenes* . . . .
. . . . . . *Laomenes mudirostris* (Bruce, 1968)
— Epistome without horns. 10

10. Dactyli of ambulatory pereiopods with hoof-shaped basal protuberance not disappearing from view when dactyl bent backwards; body strongly depressed; rostrum armed with teeth; major second pereiopod with two or three teeth on opposable margin of movable finger; rostrum with lateral carina rather abruptly expanded posteriorly into

bluntly subrectangular supraorbital eave. *Jocaste*. . . . . . *Jocaste lucina* (Nobili, 1901)
— Dactyli of ambulatory pereiopods without basal protuberance, sometimes broadened in basal region, but broadened part disappears in slit of propodus when dactylus bend backwards. 11

11. Pleura of at least fourth and fifth abdominal somites produced as distinct sharp point; ambulatory pereiopods robust, with stout simple hooked dactylus; body strongly depressed; ventral margin of rostrum armed with teeth; carapace with antennal spine considerably ventral to orbital angle, at same level as hepatic spine; second pereiopod dactylus with lateral carina and one tooth on opposable margin, fixed finger with 2 teeth, ischium with 1 distal spine on extensor margin and 2 on flexor margin. *Harpiliopsis* . .
. . . *Harpiliopsis beaupresii* (Audouin, 1825)
— Pleura of first five abdominal somites broadly rounded or bluntly pointed, never produced as sharp point; hepatic spine not moveable; rostrum laterally compressed, never flattened dorsally, so not T-shaped in transverse section, armed with teeth. . . 12

12. Basal part of rostrum with narrow lateral wings, which narrow gradually or abruptly into compressed distal part, with small dorsal teeth; ventral rostral margin unarmed; postorbital groove distinct, bordered posteriorly by postorbital carina extending from lateral margin of rostrum to near hepatic spine; carina from antennal spine extending in direction of hepatic spine; ischium and merus of ambulatory pereiopods fused. *Tulcariocaris* . . . .
Tulcariocaris holthuisi Hipeau-Jacquotte, 1965

— Rostrum without lateral wings, with conspicuous dorsal and/or ventral teeth; postorbital groove, if present, narrow, indistinct; ischium and merus of ambulatory pereiopods not fused, propodi usually spinulate; antennal spine present; second pereiopods with fingers subequal or shorter than palm, without sound-producing fossae; carapace with or without supraorbital spine; third thoracic sternite normal, not greatly elongated. 13

13. Fourth thoracic sternite with slender, finger-like median process; ambulatory pereiopods with dactylus simple, long,

slender, not hook-like; first pereiopod with fingers simple, not subspatulate. *Kemponia* 14

— Fourth thoracic sternite without slender median process; ambulatory pereiopods with dactylus simple or biunguiculate, sometimes more ornate, corpus without acute dorsodistal accessory spinules; first pereiopod with fingers sometimes subspatulate. . . 20

14. Second pereiopod merus unarmed. . . . 15

— Second pereiopod merus with distoventral tooth; ischium distoventrally unarmed; distal tooth of scaphocerite distinctly exceeding lamella. 16

15. Supraorbital spine present; second pereiopod with carpus much longer than palm. R: 1+6–9/2–3. . . . . *Kemponia anacanthus* (Bruce, 1988)

— Supraorbital spine absent; second pereiopods well developed, carpus subequal or longer than palm length, chelae more than 0.9 times carapace length, fingers with distinct diasternal notches; slenderly built species; one rostral dorsal tooth situated on carapace posterior to orbital margin; distolateral angle of basal antennular segment with distolateral tooth only; ambulatory dactylus about 0.35 times propodal length. R: 1+7–8/4–5. . . . . *Kemponia calmani* (Tattersall, 1921)

16. Supraorbital spine absent; rostrum sinuous, upcurved, greatly exceeding scaphocerite; ambulatory propods segmented, non-spinulate; distal margin of carpus of second pereiopod with one obscure teeth; R. 1+8–11/6–9. . . . . *K. tenuipes* (Borradaile, 1898)

— Supraorbital spine present; rostrum not sinuous, not greatly exceeding scaphocerite; ambulatory propods spinulate or not, nonsegmented; distal margin of second pereiopod carpus with 1–2 acute teeth. 17

17. Rostrum shallow; ambulatory pereiopods long and slender, fifth exceeding scaphocerite; carpus of male second pereiopod subequal to, or shorter than, merus. R: 1+6–8/2–4. . . . . . *Kemponia andamanensis* (Kemp, 1922)

— Rostrum moderately deep; ambulatory pereiopods relatively stout, fifth not exceeding scaphocerite. 18

18. Carpus of second pereiopod with single distomedial tooth only. R: 1+5–9/2–5. *Kemponia grandis* (Stimpson, 1860)

— Carpus of second pereiopod with two acute distal teeth. 19

19. Ambulatory pereiopods with propodi strongly spinulate; chela of second pereiopod (male only?) finely tuberculate. R: 1+5–7/2–3. . . . . *Kemponia elegans* (Paulson, 1875)

— Ambulatory pereiopods with propodi with small distoventral spine only; chela of second pereiopod not tuberculate. R: 1+6–7/3. . . . . . *Kemponia amymone* (De Man, 1902)

20. Fourth thoracic sternite with distinct acute transverse median process; second pereiopods remarkably poorly developed; ambulatory dactyli distinctly biunguiculate. R: 1+4–6/1–3. *Phycomenes* . . . . *Phycomenes zostericola* Bruce, 2008

— Fourth thoracic sternite without transverse median process; second pereiopods usually well developed; ambulatory dactyli simple or biunguiculate, sometimes more ornate. *Periclimenes* 21

21. Carapace with supraorbital or postorbital tooth; all dorsal rostral teeth situated on rostrum anterior to posterior orbital margin, with 1–3 ventral teeth; basal antennular segment armed with two distolateral spines; second pereiopod with fingers about as long as palm. . . . . *Periclimenes commensalis* Borradaile, 1915

— Carapace without supraorbital or postorbital tooth, at most with obscure tubercle. 22

22. Epigastric spine or posterior-most tooth of dorsal rostral series arising from carapace at or posterior to level of hepatic spine. . 23

— Posterior-most tooth of dorsal rostral series arising from carapace at or anterior to level of hepatic spine, not widely separated from rest of series; second pereiopod without acute distal tooth on flexor margin of merus; hepatic spine not extending beyond anterior margin of carapace; telson with two pairs of dorsal spines; ambulatory propodi without longitudinal rows of clusters of long setae on flexor margin. 26

23. Third abdominal tergite with posterior margin minute denticulate; third pereiopod dactylus clearly biunguiculate, propodus sparsely setose, two similar long distoventral spines about 0.3 times dactylar length. R: 1–2+7–8/2–3. . . . . *Periclimenes sarkanae* Bruce, 2007

— Third abdominal tergite with posterior margin entire; second pereiopod without distal tooth on flexor margin of merus; rostrum not extremely deep, dorsal and ventral margins if convex never strongly, dorsal margin not serrated with small equidistant teeth; third pereiopod with dactylus biunguiculate; orbital angle subovate, with or without acute tip; posterior-most tooth of dorsal rostral series more widely separated from next anterior tooth than any other pairs of adjacent teeth. 24

24. Abdomen with low, compressed median prominence on third somite; antennal scale less than three times as long as wide, with lateral margin straight; hepatic spine larger than antennal spine; body slender; median margin of coxae of third and fourth pereiopods unarmed, ambulatory dactyli with unguis markedly longer than accessory tooth, two or more spines on the ventral margin of propodi distributed along length; carpus of second pereiopod shorter than palm, both fingers with proximal diastema (distinct proximal concavities), dentition 1/1; patch on tergum of third abdominal somite V-shaped in dorsal view, anterior and posterior margins fringed with red lines; carpus of first pereiopod distinctly shorter than chela; cornea with ocellus, ophthalmic somite with 'bec ocelaire'; antepenultimate segment of third maxilliped without distolateral spine. R: 1–2+7–9/1–2. . . . .
. . . . . . *Periclimenes holthuisi* Bruce, 1969
— Abdomen without compressed prominence on third somite. 25

25. Second pereiopods unequal, dissimilar, carpus distinctly shorter than palm; rostrum with dorsal margin convex but not as a strongly arched lamella, ventral margin armed with two teeth, not small, placed posterior to level of at least one dorsal marginal tooth; epigastric spine and posterior-most rostral tooth articulated; first pereiopod chela slightly shorter than carpus, distinctly shorter than merus, not longer than carpus; propodus of third pereiopod armed distally with three pairs of long slender spines, length exceeding distal propodal width, and single long ventral spine, with two distal pairs only. R: 2+7/2. . . *Periclimenes terangeri* Bruce, 1998

— Second pereiopod with carpus more than 1/2 as long as palm, merus of major second pereiopod not overreaching rostrum; rostrum not very deep, horizontal, not exceeding intermediate segment of antennular peduncle, ventral margin armed with small teeth, placed below or anterior to foremost dorsal marginal tooth; pereiopods not remarkable elongate and slender; antennal scale more than three times as long as wide; body size relatively small; fingers of first pereiopod not much longer than palm; epigastric spine at anterior 0.3 of carapace length; telson with small acute median process on posterior margin. R: 1+7/0. . . . .
Periclimenes cobourgi Bruce & Coombes, 1995

26. Third pereiopod with dactylus biunguiculate, accessory tooth minute, without denticle on flexor margin of dactylus; basal antennular segment armed with 2 or 3 distolateral teeth, stylocerite not reaching as far as articulation of second peduncle segment; antennal spine directed anteriorly, not dorsally; rostrum not typically palaemonoid, compressed, dorsal teeth anteriorly crowded, ventrally with convex keel and lacking teeth; sixth abdominal somite less than twice as long as fifth; antennal scale about 2.3 times longer than wide, lateral margin nearly straight, distolateral tooth not nearly reaching level of distal margin of blade, fingers of first pereiopod pectinate on opposable margins. R: 10–13/0. . . . . .
. . . . *Periclimenes soror* Nobili, 1904
— Third pereiopod with dactylus simple, not biunguiculate; second pereiopod with fingers subequal to or shorter than palm; first pereiopod with fingers usually subequal to palm; fourth thoracic sternite without large linguiform median plate; unguis of ambulatory dactylus unarmed. 27

27. Rostrum with midrib directed somewhat anteroventrally, not overreaching antennal scale, dorsal margin of rostrum faintly convex, all dorsal rostral teeth confined to rostrum anterior to orbital margin, posterior-most dorsal rostral tooth not distinctly smaller than anterior teeth; third pereiopod without subdistal projection on flexor margin of dactylus; anterior pair of telson dorsolateral spines situated at about a third of length; hepatic spine arising only slightly below level of antennal spine; sixth abdom-

inal somite 1.5 times as long as fifth; first pereiopod with fingers pectinate on opposable margins; second pereiopod with carpus little longer than distal width; body larger. Associated with giant anemones; almost completely colourless. . . . . . .
. . . . . *Periclimenes inornatus* Kemp, 1922

— Rostrum with midrib nearly horizontal, directed more anteriorly than anteroventrally, dorsal margin distinctly convex. . 28

28. First pereiopod with fingers pectinate on opposable margins; second pereiopod with fingers nearly as long as palm, carpus 1.5 times longer than distal width. . . . .
. *Periclimenes brevicarpalis* (Schenkel, 1902)

— First pereiopod with fingers not pectinate on opposable margins, simple, not subspatulate; second pereiopods markedly unequal, cutting edges of fingers with one tooth on dactylus and two on fixed finger; rostrum relatively shallow. . . . .
. . . . *Periclimenes ruber* Bruce, 1982

29. Dactyli of ambulatory pereiopods with distinct basal protuberance not disappearing from view when dactylus bent backward. 30

— Dactyli of ambulatory pereiopods without basal protuberance, base of dactylus sometimes broadened, but broadened part disappearing in slit of propodus when dactylus bent backward; rostrum may be reduced but not almost obsolete; scaphocerite not aciculate, lamella not obsolete; first pereiopods equal, carpus not segmented. . . . 32

30. Basal protuberance on dactylus of ambulatory pereiopods compressed or rounded, not hoof-shaped; body rounded or depressed; antennal spine absent; rostrum depressed, toothless; fingers of second pereiopod normal, not excavated on inner surface; ambulatory dactylus armed with two strong, divergent, spine-like teeth, basal process well developed, without marginal tooth; lateral posterior spines of telson situated at apex; first pereiopod with carpus distinctly shorter than merus; rostrum not reaching end of scale. *Conchodytes* . . . .
. . . . *Conchodytes meleagrinae* Peters, 1852

— Basal protuberance on dactylus of ambulatory pereiopods hoof-shaped; body strongly depressed; antennal spine present. *Coralliocaris* 31

31. Lateral margin of dactylus of second pereiopod strongly convex and semicircular; first pereiopods slender, chela about four times as long as wide; basis of first pleopod with flattened setae on dorsal surface in males and young; posterior ventral angle of fifth abdominal somite acute. R: 4–5/1–2. . . . .
. . . . . *Coralliocaris graminea* (Dana, 1852)

— Lateral margin of dactylus of second pereiopod abruptly angled, cutting edge of fixed finger with 2 teeth; third maxilliped with penultimate segment less than twice as long as wide; dactylus of third to fifth pereiopods tipped with small projection, hook-shaped protuberance strong. R: 4–5/1–2. . . . .
. . . . . *Coralliocaris superba* (Dana, 1852)

32. Rostrum depressed, toothless, lateral carinae distinctly expanded, reaching well beyond eyes; pterygostomian angle rounded, not distinctly produced anteriorly; antennal spine present; second pereiopods very unequal, fingers of major distinctly dentate, dactylus with flange-like ridge in upper half of lateral surface, carpus of major cup-shaped, hardly longer than wide, carpus of minor slender, more than four times longer than wide; both pairs of dorsolateral telson spines very small, placed in posterior half of telson; peduncles of eyestalks not fully exposed dorsally, orbit developed, with postorbital notch, inferior orbital angle indistinct; first segment of antennular peduncle with massive ventromedial tooth; first maxilliped with palp; third maxilliped without arthrobranch; first pereiopod with fingers spatulate; third pereiopod with dactylus not compressed, corpus not distally laminar, distinctly bidentate, unguis indistinct, propodus without strong denticulate club-shaped distoventral and ventral spines. *Pontoniopsis* . .
. . . *Pontoniopsis comanthi* Borradaile, 1915

— Rostrum laterally compressed, usually with teeth. 33

33. Second pereiopods equal or unequal, fingers without molar-like tooth and fossae; dactylus of third pereiopod similar to those of fourth and fifth, not more than four times long than broad, less than half as long as propodus; if dorsal teeth present on rostrum then all anterior to orbital margin.
. . . . 34

— Second pereiopods very unequal in size and shape, dactylus of major with molar-shaped tooth, fixed finger with fossae; exopod of uropod with distolateral tooth and mobile spine medially; carapace without post-antennal spines. *Periclimenaeus*. . . 36

34. Exopod of uropod with several slender teeth on external margin and external part of diaeresis; supraorbital teeth absent. R: 5/1. *Apopontonia* . . . . *Apopontonia dubia* Bruce, 1981

— Outer margin of uropodal exopod straight, ending in single posterior tooth, with single, very small, uncurved movable spine at its inner side on extreme outer part of diaeresis; telson normally with two pairs of dorsal spines; posterolateral angle of sixth abdominal somite rounded or triangular, not spinous. 35

35. Telson with anterior pair of dorsal spines on anterior half; dactylus of ambulatory pereiopods, apart from end claws, with many small denticles on posterior margin; palm of first pereiopods about four times as long as fingers; rostrum unarmed; ventral angle of orbit rounded, not spinose; second pereiopod with distal tooth on flexor margins of merus and ischium, fixed finger at most indistinctly and unequally bifid at distal end; cornea of eye hemispherical; third pereiopod with dactylus unarmed on flexor margin of unguis. *Onycocaris* . . . . *Onycocaris stradbrokei* Bruce, 1998

— Telson with both pairs of dorsal spinules in posterior half; dactylus of ambulatory pereiopods simple; palm of first pereiopods about as long as fingers, chela unusually curled to form open tube; rostrum distally compressed laterally, unarmed; antennal spine usually present; carapace with minute antennal spine; third maxilliped with antepenultimate segment about twice as wide as penultimate segment. *Anchistus* . . . . *Anchistus custos* (Forskål, 1775)

36. Distal cutting edge of dactylus of minor second pereiopod denticulate; unguis of dactylus of third pereiopod without transverse rows of small tubercles proximodorsally, corpus distally unarmed. . . . 37

— Distal part of cutting edge of dactylus of minor second pereiopod entire; distal part of cutting edge of dactylus of major second pereiopod entire; small species. 38

37. Dactylus of ambulatory pereiopods without acute tooth on proximal border of corpus; dactylus of major second pereiopod at most slightly longer than fixed finger; dactylus of minor second pereiopod with about 40 small teeth along whole cutting edge. R: 4–5/0. . . . . *Periclimenaeus hecate* (Nobili, 1904)

— Dactylus of ambulatory pereiopods with acute tooth on proximal border of corpus; dactylus of third pereiopod with proximal tooth perpendicular to margin, propodus without spines except for two distolateral ones; dactylus of major second pereiopod with cutting edge entire. R: 3/0. . . . . *Periclimenaeus myora* Bruce, 1998

38. Carapace with acute supraorbital spine, but not very large; first pereiopod short and stout, merus not far exceeding scaphocerite; body about 10 mm total length; rostrum armed with less than eight teeth; dactyli of ambulatory pereiopods normal, not very elongate and slender, much less than half of propodus length, unsegmented, without small blunt teeth on distoventral margin. . . . . *Periclimenaeus zanzibaricus* Bruce, 1969

— Carapace without distinct supraorbital or supraocular spines, with supraorbital tubercle; dorsal surfaces of chelae of second pereiopods not armed with long slender spines, at most with small tubercles or denticles, tips of dactyli distinctly doubled; dactylus of first pereiopods of similar length to fixed finger, palm not distinctly ventromedially curved. . . . . *Periclimenaeus bidentatus* Bruce, 1970

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Sphaeromatid isopod (Crustacea: Peracarida) assemblages in an algae-sponge association at North Stradbroke Island, southeastern Queensland

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ABSTRACT

The endofauna of the green algae *Cladophoropsis vaucheriaeformis* (Aresch.) Papenf. was examined. This algae is associated with sponge tissue and has a tough, spongious thallus morphology. Twenty thalli were sampled in shallow waters of 1–9 m near Amity Point, North Stradbroke Island, Queensland, of which five samples were found to be inhabited by large numbers of sphaeromatid isopods belonging to the species *Oxinasphaera lobivia*, Bruce 1997. This is the first time assemblages of the isopod *O. lobivia* are reported in association with the algal-sponge association *Cladophoropsis vaucheriaeformis*. ❏ symbiosis, algae, sponge, Crustacea, Peracarida, Isopoda, Queensland, Australia

The green algal genus *Cladophoropsis* is widely distributed in warm-temperate and tropical waters of the Atlantic, Indian and Pacific Oceans. The genus was created by Børgesen (1905) and a recent revision resulted in the recognition of 6 morpho-species, although recognising that generic relationships with other taxa in the Siphonocladales require further attention (Leliaert & Coppejans 2006). *Cladophoropsis vaucheriaeformis* (Aresch.) Papenf. is an unusual member of the genus because of its association with sponge tissue. This sponge association results in a tough, spongiose thallus morphology and an atypical branching pattern. *Cladophoropsis vaucheriaeformis* generally grows epilithically, occasionally on calcified seaweeds in the mid-intertidal to shallow subtidal down to 1 m (Leliaert & Coppejans 2006). At Amity Point, North Stradbroke Island, Queensland, *Cladophoropsis vaucheriaeformis* is found on most stones in the sandy bay.

Isopods are well known as parasites of both fishes and crustaceans (e.g. see Rhode 2005),

but other forms of opportunistic or obligate symbioses are relatively rare. Examples include the cirolanid *Cartetolana integra* (Miers, 1884) (Bruce 1986) which inhabits the anal cavity of tropical crinoids, *Neocirolana hermitensis* (Boone, 1918), another cirolanid, lives in association with hermit crabs (Bruce 1994), and the corallanid *Argathona rostrata* Bruce, 1982, which inhabits sponges. Species of Sphaeromatidea are not frequently known as symbionts or associates of other biota. Within the family Sphaeromatidae the monotypic *Xynosphaera* Bruce, 1994, has morphological adaptations for a symbiotic association with alcyonceans; *X. colemani* Bruce, 1994, burrows into the host although the exact trophic relationship is not known. Sphaeromatid association with sponges are more widely reported, notably the species *Paracerceis sculpta* (Holmes, 1904) (see Shuster 1992; Shuster & Sassaman 1997) while *Cassidias* sp. has been reported from gorgonian corals (Bruce 1999). In contrast to these sparse records of isopod-sponge

association, the Indo-West Pacific genus *Oxina-sphaera* Bruce, 1997, is known to have numerous species associated with sponges or which have been directly collected from or in association with sponges, 'sponges' being the most commonly recorded habitat for species of the genus. In most cases the identity of the host sponges is not known, and therefore the level of host specificity or degree of host preference remains unknown.

MATERIAL AND METHODS

In February 2005, during the Moreton Bay Marine Biodiversity workshop, 20 thalli of *Cladophoropsis vaucheriaeformis* were sampled at Amity Point via snorkelling. The pieces were cut off at the base with a knife and each algal piece placed in a fine-mesh (0.30 mm) bag.

In the laboratory the volume of each sample was determined by water replacement in a measuring cylinder. The associated epifauna was collected and identified to OTU and to species where possible. The fauna found living within the anastamosing network of the *Cladophoropsis* thalli was revealed by carefully slicing the algae under a stereomicroscope; the isopods were directly removed, counted and identified.

RESULTS

Five of the twenty pieces of *Cladophoropsis vaucheriaeformis* contained sphaeromatid isopods, all belonging to the species *Oxinasphera lobivia*. The volume of the *Cladophoropsis* ranged from 85–410 ml, the number of sphaeromatids, not directly related to the volume of the alga, ranged from 15–506 individuals. A total of 811 specimens of *Oxinasphaera lobivia* were found in

the five algal pieces, see Table 1. Males, females and juveniles of *Oxinasphera lobivia* were found within the tissue mass of *Cladophoropsis*. The average host volume per individual sphaeromatid varied from 0.8 ml to 13.3 ml, with an average of one sphaeromatid per 1.4 ml algae tissue.

The 15 pieces of *Cladophoropsis vaucheriaeformis* not containing sphaeromatids were not inhabited by any other macro-invertebrates. Occasional Tanaidacea and Amphipoda were found externally on the algae-sponge association, but not inside. The volume of the 'empty' *Cladophoropsis* samples varied from 10–350 ml. Overall the epifauna of the *Cladophoropsis* hosting sphaeromatids and those without inhabitants was very similar.

DISCUSSION

Oxinasphaera lobivia Bruce, 1997, is a known associate of sponges, although sponge identity has not been recorded (Bruce 1997). *O. lobivia* is here reported in association with the algal-sponge association of *Cladophoropsis vaucheriaeformis* for the first time. We believe *O. lobivia* is primarily using the algae-sponge association as a refugium, not as a direct food source. Even though we have not conducted stomach content analysis, the host tissue did not seem to be affected by its inhabitants. At least while slicing the algae pieces, no apparent difference in structure was obvious between *Cladophoropsis* hosting sphaeromatids and those without inhabitants.

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TABLE 1. Number of *Oxinapshaera lobivia* per sample of *Cladophoropsis vaucheriaeformis* at Amity Point, North Stradbroke Island, Moreton Bay.

Sample	Feb 05	Lat/Long	Depth (m)	*C. vaucheriaeformis* (ml)	*O. lobivia* no. of specs
A8-04	14	27º23.9'S 153º26.2'E	5–10	150 ml	80
A9-12	15	27º24.25'S 153º26.22'E	4–9	85 ml	106
A9-13	15	27º24.9'S 153º26.22'E	4–9	410 ml	506
A20-03	20	27º23.9'S 153º26.2'E	0.5	200ml	15
A20-09	20	27º23.9'S 153º26.2'E	0.5	260 ml	104

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Loxothylacus spinulosus (Crustacea: Cirripedia: Rhizocephala) parasitising Pilumnopeus serratifrons (Decapoda: Pilumnidae) in Moreton Bay, Queensland, Australia

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ABSTRACT

Seventy-eight individuals of the cryptic pilumnid crab Pilumnopeus serratifrons inhabiting galleries in clumps of mussels (Trichomya hirsutus) (Mytilidae) were collected from intertidal sea grass beds seaward of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, Australia. Of the 78 crab individuals, five of the 45 males (11.1%) and 14 of the 33 females (42.4%) were parasitised by the rhizocephalan Loxothylacus spinulosus. No gravid females were parasitised, but the parasite appeared to restrict the size range of such females to carapace widths of between 7.5–10.0 mm. No gravid female > 10.0 mm carapace width was identified, all such individuals presumably being castrated by L. spinulosus. One male and four females had two parasite externas. ❑ Pilumnopeus serratifrons, parasitised, rhizocephalan, Loxothylacus spinulosus, Moreton Bay, Australia.

The biology of rhizocephalan barnacles has been reviewed by Høeg & Lützen (1995). Parasitic rhizocephalans have a planktonic larval phase that normally involves several naupliar stages and a cyprid settling stage. Adults are internal parasites of mainly marine shrimps and crabs. The rhizocephalan life cycle is hence both complex and specialised such that the ecologies of host and parasite are highly correlated. Rhizocephalan larvae are dioecious, males being often smaller than females. The life cycle begins with the female cyprid invading a crustacean host and developing into a parasite with an internal root system (interna) that grows inside it and absorbs nutrients. Once the interna matures, it will develop a reproductive body (externa) outside the crab through the region of the abdomen. Male cyprids will then enter the young (virgin) externa that gives rise to a fertilised externa with the eggs brooded inside it. Larvae will eventually be released via the externa.

There are few records of species of rhizocephalans parasitising decapod crustaceans in Australian waters. In Moreton Bay, however, the commercial sand crab Portunus pelagicus (Linnaeus, 1758) is parasitised by Sacculina granifera Boschma, 1973, and has thus received particular attention (Phillips & Cannon 1978; Bishop & Cannon 1979; Weng 1987; Shields 1992; Shields & Wood 1993; Sumpton et al. 1994; Gaddes & Sumpton, 2004). Phillips (1978), however, described three new species of rhizocephalan from Moreton Bay. These were Heterosaccus lunatus, H. multilacinensis and Sacculina amplituba parasitising the portunid crabs Charybdis callianassa

(Herbst, 1801), *Charybdis truncata* (Fabricius, 1798) and *Matuta granulosa* Miers, 1877, respectively. Knuckey *et al.* (1995) recorded *Loxothylacus ihlei* (Boschma, 1949) infecting the commercial portunid mud crab *Scylla serrata* (Forskål, 1775) in northern Australia, but while the host is common in Moreton Bay, the parasite appears to be restricted to tropical waters. The present study concerns *Loxothylacus spinulosa* Boschma, 1928, parasitising the pilumnid crab *Pilumnopeus serratifrons* (Kinahan, 1856).

MATERIAL AND METHODS

From 7–25 February 2005, visits were made during low tide periods to the sea grass (*Zostera capricorni*, *Halodule uninervis* and *Halophila ovalis*) beds down-shore from the mangrove-fringe at Myora Springs on the sheltered northwest coast of North Stradbroke Island. The principle research aim was to study a sympatric pair of galeommatid bivalves (*Varotoga* spp.) living commensally within the galleries made by the crab *Pilumnopeus serratifrons* in clumps of the mussel *Trichomya hirsutus* (Lamarck, 1819), that here dot the central regions of the muddy, sea grass dominated, intertidal. This research has been separately reported upon by Morton (2008). *Pilumnopeus serratifrons* was, however, noticeably parasitised by a rhizocephalan cirripede herein identified as *Loxothylacus spinulosus*. The sex of each crab was recorded and carapace widths measured to the nearest 0.5 mm using vernier calipers. The presence of either a crab egg mass or the externa of *L. spinulosus* was also noted.

The identification of rhizocephalan species is difficult and often relies upon identification of the host, as many are considered to be host-specific, as well as upon microscopic investigation of histological sections through the externa. Accordingly, two externae were removed from their hosts, sectioned longitudinally at 8 μm, and stained with Ehrlich's haematoxylin and eosin.

RESULTS

TAXONOMIC REMARKS

Loxothylacus is characterised by having the stalk and mesentery inserted at different places on the mantle (Boschma 1933: fig. 9), and the curved male receptacles have their terminal spermatogenic components included within the ovary. Also, as may often occur in kentrogonid rhizocephalans, only one of the receptacles was producing semen.

The external mantle cuticles of the present specimens were scattered with spiny excrescences (5–6 mm), as described for *Loxothylacus spinulosus* by Boschma (1933: fig. 10). The presence of such relatively short excrescences is characteristic of *L. spinulosus* (and *L. omissus* Boschma, 1957). Most other species of the genus have longer structures often arranged in bundles, although three species, *L. scaber* (Boschma, 1931), *L. bicorniger* Boschma, 1959, and *L. engeli* Boschma, 1968, all have a smooth (or nearly so) external cuticle (Boschma 1968). Both sectioned rhizocephalans correspond in all essential characters to the two specimens of *L. spinulosus* described by Boschma (1928, 1957).

Loxothylacus spinulosus is known only from eastern Australian waters. The only two earlier records are also from *Pilumnopeus serratifrons*: one from Mosman, Sydney, New South Wales, the other from an unknown locality (Boschma 1957). Two specimens originally identified as *L. spinulosus* were described from Hong Kong as infecting *Glabropilumnus seminudus* (Miers, 1884) (Boschma 1955), but subsequently described as a separate species, *L. omissus* Boschma, 1957.

BIOLOGY

A total of 78 individuals of *Pilumnopeus serratifrons* was collected. Of these, five of the 45 males (11.1%) and 14 of the 33 females (42.4%) were parasitised by *Loxothylacus spinulosus*. None of the nine gravid females (27.3%) was parasitised. The mean carapace widths of parasitised male and female individuals of *P. serratifrons* were 10.0 mm and 10.3 mm respectively, as opposed to the mean widths of uninfected conspecifics that were 5.6 mm and 8.3 mm respectively. Of the five parasitised males, four had one parasite and one had two. Of the 14 parasitised females, 10 had one parasite and four had two (Table 1). Gravid females were, however, restricted to a carapace width size range of between 7.5–10.0 mm, all individuals of greater widths being parasitised and reproductively sterile, presumably as a consequence of the rhizocephalan infection.

Table 1. The numbers of individuals of each sex of *Pilumnopeus serratifrous* from the shore at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, infected with *Loxothylacus spinulosus*.

	Number	Mean carapace width (mm)	Range in carapace width (mm)	Mean width of unparasitised individuals (mm)	Mean width of parasitised individuals (mm)	Numbers of *Loxothylacus* (with 1 **or** 2) + %
Males	45	7.3	3.5–14.5	5.6	10.0	5 (4 **or** 1) + 8.9
Females	33	9.2	5.5–14.0	8.3	10.3	14 (10 **or** 4) + 42.4
Gravid females	9	8.7	7.5–10.0	–	–	–

DISCUSSION

Sacculina carcini Thompson, 1836, prefers to attack the host crab, *Carcinus maenas* (Linnaeus 1758) at the intermoult rather than the recently moulted stage (Glenner & Werner 1998). Many species of *Sacculina* are host specific, as with those described from Moreton Bay by Phillips (1978), while others are not. Thus, Liu & Lutzen (2000) have shown that in Taiwan, *Sacculina plana* Boschma, 1933, parasitises six species of grapsid crabs including the rocky shore species *Grapsus albolineatus* Lamarck, 1818, *G.* [= *Cyclograpsus*] *intermedius* De Man, 1888, and *G. longitarsis* Dana, 1851. Prevalence ranged from 13.4–71.7% in *G. albolineatus*, with males and females being generally equally infected. Thresher *et al.* (2000) showed that *Sacculina carcini* was unable to attack native crabs in its introduced range of Australia. In contrast, Goddard *et al.* (2005) showed that *S. carcini* introduced to North America, infected native hosts, at rates ranging from 35–52%, but that the crabs arrested the infection early by melanising the rootlets of the parasite and all such infected native crabs died without producing an externa. Interestingly, in European waters where *S. carcini* is indigeneous, it may infect up to 11 crab species belonging to five genera (Høeg & Lützen 1985). Sumpton *et al.* (1994) have shown that in Moreton Bay females of *Portunus pelagicus* are more liable to infection (12.3%) by *S. granifera* than males (7.0%), although Weng (1987) obtained contrasting results for the same species. In the present study, female *Pilumnopeus serratifrous* were over-ridingly selected by *Loxothylacus spinulosus* although, as for *S. granifera* parasitising *P.*
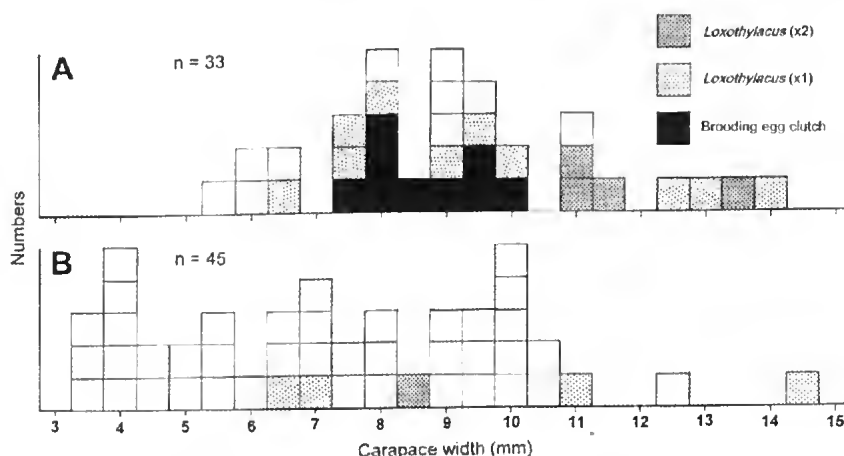
FIG. 1: Histograms showing the population structure (in terms of carapace widths) of **A**) female, and **B**) male *Pilumnopeus serratifrous* individuals in the mussel (*Trichomya hirsutus*) clusters on the shore at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland. Also identified are gravid (egg bearing) females and individuals parasitised by either one or two *Loxothylacus spinulosus* individuals.

pelagicus (Sumpton *et al.* (1994), the size distributions of infected and uninfected individuals were the same.

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Excavation, habitation and transportation of massive corals by the crab *Actumnus setifer* (Crustacea: Brachyura: Pilumnidae) in Moreton Bay, Queensland

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ABSTRACT

Previously unreported coral-carrying, and coral-burrowing, behaviour is described and illustrated for *Actumnus* se*tifer* from Moreton Bay, Queensland, Australia. *A.* se*tifer* typically inhabits excavated burrows in living or dead massive coral clumps that weigh as much as one kilogram or more. Records of this behaviour in other species are discussed. Taxonomy is briefly reviewed and full synonymy and distribution records presented. Morphological modifications that allow such behaviour may be important in generically revising the genus *Actumnus*. The sheltered coral reefs of Moreton Bay provide an ideal environment for this crab-coral association to flourish. ❑ *symbiosis, mutualism, Actumnus, behaviour, coral reef, taxonomy.*

An interesting commensal association between crabs of the genus *Actumnus* and a variety of corals, whereby the crab excavates a burrow in the base of the coral clump and moves the coral from place to place, has been reported several times. Ward (1942) first noted this behaviour for *Actumnus anteluuei* Ward, 1942, inhabiting dead corals at Mauritius, while also mentioning that he had seen a similar species behaving in the same way at Lindeman Island, on the Great Barrier Reef, using living colonies of *Leptastrea bottae*, and on reefs off Papua. Later, Lamberts & Garth (1977) reported *A. anteluuei* and *A. digitalis* (Rathbun, 1907) inhabiting 12 species of both living and dead corals at Tutuila, American

Samoa. Marsh (1990) also reported an unidentified Xanthoid crab found in a species of *Cyphastrea* coral at Shark Bay, Western Australia, that in all likelihood would also have been an *Actumnus* species.

Actumnus setifer (de Haan, 1835) has a widespread Indo-West Pacific distribution, and a bathymetric range generally < 50 m (Sakai 1976). Although it is commonly associated with coral reef environments it has not been previously recorded as inhabiting a moveable coral shelter. Its habitat has been previously noted as holes made in soft stones (Lanchester 1900), rock or coral crevices, amongst algae and in holes in sponges (Sakai 1976). We here describe and illus-

trate previously unreported coral-burrowing and coral-carrying behaviour of *A. setifer* observed in Moreton Bay, Australia.

Moreton Bay lies at latitude 27°25′ S. It is 150 km long (north to south) and about 15 km wide at the northern end where it opens to the South Pacific Ocean. It is enclosed on its eastern margin by large islands of Pleistocene and Holocene dune sands. The southern bay is congested with low deltaic mangrove islands, and high islands of similar lithology to the adjacent mainland occur in the central Bay. In the more open, northern parts of Moreton Bay, coral reefs have developed adjacent to the mainland and several of the islands. Many areas of these reefs have degraded during the late Holocene period, probably as a result of diminished tidal flushing, the changed position of the Brisbane River mouth, and a slight fall in relative sea level (Lovell 1989; Stephens 1992; Johnson & Neil 1998) and, more recently, due to increased sediment concentrations in the Brisbane River due to land use change (Neil 1998). Reefal environments of Moreton Bay have also been exploited for lime-making for more than a century (Allingham & Neil 1995).

TAXONOMY

Family Pilumnidae Samouelle, 1819

Actumnus Dana, 1851

Actumnus Dana, 1851: 128. Type species: *Actumnus tomentosus* Dana, 1852, by subsequent designation of Rathbun (1922); gender masculine [= *Actumnus setifer* (De Haan, 1835)].

Remarks. The genus currently includes 28 species (see Ng *et al.* 2008).

Actumnus setifer (de Haan, 1833)
(Figs 1, 3)

Cancer (Xantho) setifer de Haan, 1833: pl. 3, fig. 3; Yamaguchi, 1993: 580.
Cancer (Pilumnus) setifer — de Haan, 1835: 50.
Actumnus tomentosus Dana, 1852: 243; 1855: pl. 14, fig. 2a–c; Milne-Edwards A., 1865: 285; 1873: 194; Haswell, 1882: 73; Alcock, 1898: 202; Borradaile, 1902: 249; Nobili, 1906b: 132; Grant & McCulloch, 1906: 17; Klunzinger, 1913: 271; Rathbun, 1924: 20.
Actumnus setifer — Milne-Edwards, A., 1865: 287, pl. 15, fig. 5; Richters, 1880: 148; Miers, 1884: 225; de Man, 1887a: 47; Walker, 1887: 110; de Man, 1887b:

262; Pocock, 1890: 74; Henderson, 1893: 364; Ortmann, 1893: 474; 1894: 52; Alcock, 1898: 202; Calman, 1900: 19; Lanchester, 1900: 742; 1902: 541; Borradaile, 1902: 249; de Man, 1902: 639; Nobili, 1906a: 285; Grant & McCulloch, 1906: 17; Rathbun, 1910: 357; 1911: 230; 1914: 660; 1923: 126; Klunzinger, 1913: 272; Balss, 1922: 119; 1924: 20; 1933: 38; Yokoya, 1933: 187; Sakai, 1934: 309; 1935: 70; 1936: 173, pl. 52, fig. 1; 1936: 67; 1939: 528, pl. 65, fig. 1; 1965: 156, pl. 76, fig. 6; 1976: 496, pl. 177, fig. 2; Shen, 1940: 72, 87; Stephensen, 1945: 143; Miyake, 1961: 173; Takeda & Miyake, 1969: 115, fig. 9d–f; Campbell & Stephenson, 1970: 285, fig. 46; Takeda & Nunomura, 1976: 76; Yamaguchi *et al.*, 1976: 38; Takeda, 1977: 86; 1989: 166; 1997: 246; Miyake, 1983: 133, pl. 45, fig. 1; Dai & Yang, 1991: 369, fig. 179(1), pl. 49(7); Yamaguchi & Baba, 1993: 454, fig. 170; Wada, 1995: 402, pl. 112, fig. 1; Muraoka, 1998: 45.
Actumnus setifer var. *tomentosus* — Laurie, 1906: 408; 1915: 458.
Actumnus setifer var. *setifer* — Laurie, 1906: 409.
?*Actumnus setifer* — Barnard, 1947: 365; 1950: 271, fig. 50.

Material Examined. QM-W28544, male (24.0 x 17.0 mm), 2 females (18.3 x 13.2; 21.3 x 14.8 m), Wellington Point, Moreton Bay, SE Qld, 27°28′0″ S, 153°14′0″ E, low intertidal, P. Davie, I. Fellegara, 30 Jul 2008, under and in dead coral colonies of *Favia speciosa*. QM-W16680, ovig. female (17.5 x 12.2 mm), King Reef, off Kurrimine Beach, NE Qld, 17°45′0″ S, 146°9′0″ E, trawled, K. Lamprell, 29.07.1983. QM-W21176, female (11.8 x 9.0 mm), Long Is, Vansittart Bay, Kimberley Coast, WA, 13°58′ 9″ S, 126°19′ 6″ E, J.W. Short, 24.11.1995. W27453, 3 males (22.0 x 16.8, 22.4 x 17.1, 22.6 x 17.4 mm), Mirs Bay, New Territories, Hong Kong, 22°55′0″ N, 114°40′ 0″E, agassiz trawl, P. Davie, 26.04.1989.

Diagnosis. Deep-bodied crab; dorsal surface convex, regions clearly defined; carapace covered with short-cropped tomentum; frontal lobes markedly deflexed; anterolateral margins convex, with three pointed teeth behind exorbital angle, more or less obscured by tomentum; posterolateral borders markedly excavated, forming concavity into which last pair of ambulatory legs fold. Chelipeds markedly unequal; covered with dense short tomentum; carpus and propodus covered with irregular beaded granules projecting through tomentum. Ambulatory legs relatively short and stout; anterior and posterior borders thickly fringed with setae.

Distribution. Type locality Japan. Widespread from South Africa to Japan and French Polynesia. AUSTRALIA — Albany Passage (Haswell, 1882), Thursday I., Port Denison, Percy Islands and
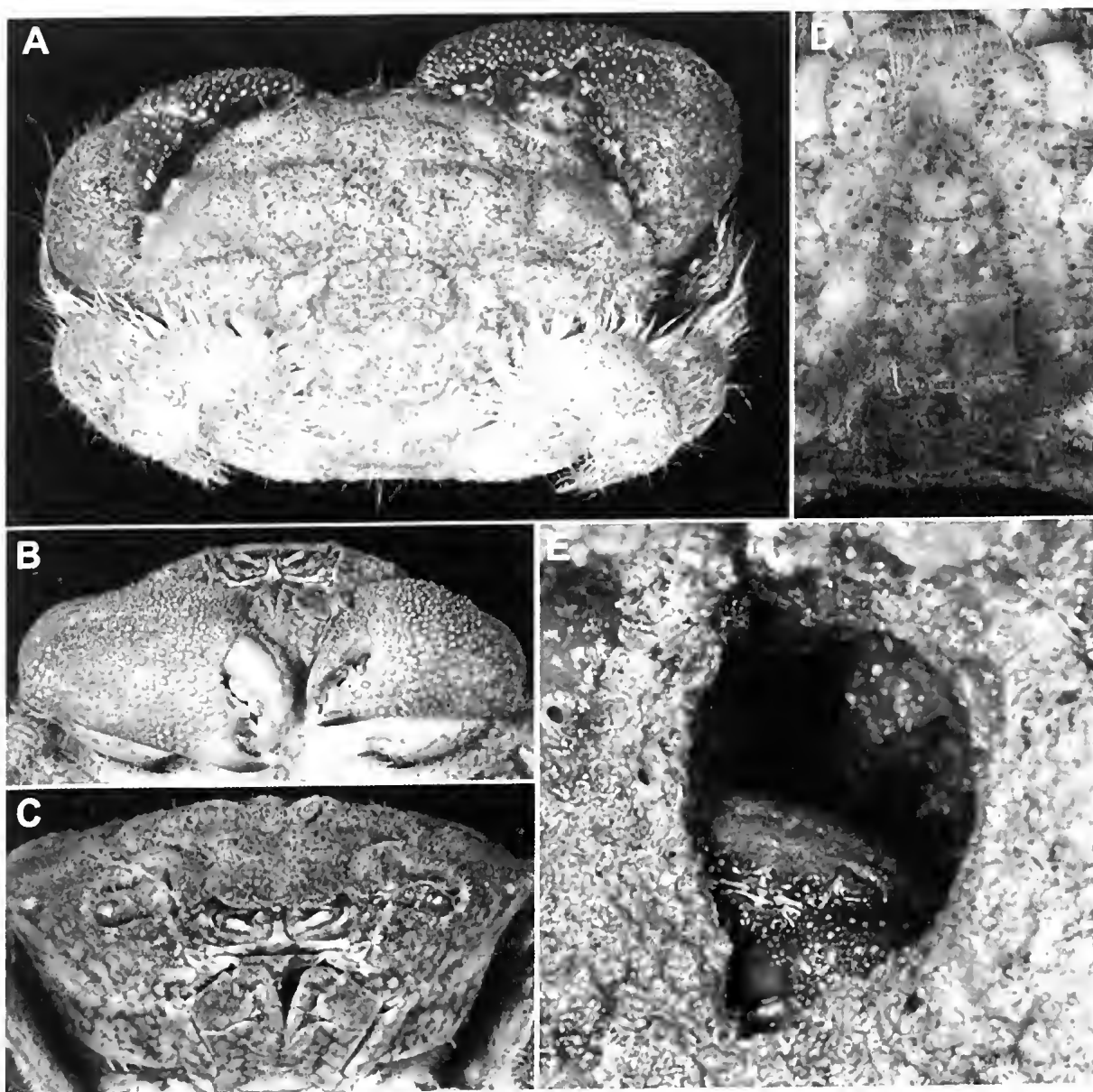
FIG. 1. *Actumnus setifer* male (24.0 x 17.0 mm) from Wellington Point, Moreton Bay (QM-W28544). **A**, dorsal view with legs folded against body in typical fashion; **B**, frontal view of claws; **C**, view of frontal margin, orbits and pterygostome; **D**, male abdomen and sternum; **E**, peering out from inside coral hole.

Sir C. Hardy's Is, Qld (Miers, 1884), Thursday I. (Ortmann, 1894), Torres Strait (Calman, 1900), Masthead I. (Grant & McCulloch, 1906), Shark Bay, WA (Miers, 1884, Balss, 1933), Monte Bello Is (Rathbun, 1914), Cape Jaubert (Rathbun, 1924), north-west of Cape Jervis and Kangaroo Island, SA (Rathbun, 1923), Moreton Bay (Campbell & Stephenson, 1970). ELSEWHERE — New Caledonia (A. Milne-Edwards, 1873, Takeda & Nuno-mura, 1976); Vanuatu (Miers, 1884); Fiji (Miers, 1884); Samoa (Ortmann, 1893, Alcock, 1898); Tahiti (A. Milne-Edwards, 1865); Tahiti or Samoa (Dana, 1852); Red Sea (Klunzinger, 1913, Laurie, 1915); Zanzibar (Nobili, 1906); ? South Africa (Barnard, 1947); Seychelles (Rathbun, 1911); Mauritius (Richters, 1880); Persian Gulf (Alcock, 1898, Nobili, 1906, Stephensen, 1945); India (Alcock, 1898); Sri Lanka (Alcock, 1898, Laurie,

1906); Maldives (Borradaile, 1902); Burma (Alcock, 1898), Gulf of Martaban (Henderson, 1893); Andaman Islands (Alcock, 1898); Mergui Archipelago (de Man, 1887a, Alcock, 1898); Japan (de Haan, 1833; Ortmann, 1893; Calman, 1900; Sakai, 1965; Balss, 1922; Yokoya, 1933; Sakai, 1935; Sakai, 1939; Miyake, 1961; Takeda & Miyake, 1969; Sakai, 1976; Yamaguchi et al., 1976; Takeda, 1977; Miyake, 1983; Takeda, 1989; Takeda, 1997); China (Alcock, 1898; Shen, 1936, 1940; Dai & Yang, 1991); Macclesfield Bank (Pocock, 1890); Gulf of Thailand (Rathbun, 1910); Singapore (Walker, 1887); Malay Peninsula (Lanchester, 1902); Philippines (Miers, 1884); Indonesia (de Man, 1887b; de Man, 1902).

Bathymetric range. Low tide pools to 200 m.

Remarks. This species was first reported from Moreton Bay by Campbell & Stephenson (1970), though their specimen was collected from a dredge and no coral association was recorded. The present specimens were compared with those from other localities in northern Australia, and from Hong Kong (see Material Examined). All Australian specimens conform closely with the Asian crabs, and there is no doubt of their correct identity. Indeed this species has been reported many times from a wide range of localities and only the identity of a specimen from South Africa reported by Barnard (1950) is currently in question — according to Sakai (1965), this specimen differs in the formation of the front, and in the armature of the anterolateral borders.

Actumnus contains 28 currently recognised species (see Ng *et al.* 2008), however there is some suggestion that the genus is not mono-phyletic as presently conceived (Takeda & Miyake 1969; P. Davie pers. observ.). Clark & Ng (2004) have also documented the complete larval development of *Actumnus setifer*. This species has only three zoeal stages instead of the more common four, and the zoeas differ from those of the only other species of *Actumnus* for which larvae are known, *A. squamosus*, in several carapace and abdominal features. Clark & Ng consider the differences important enough to indicate that the two species are not congeneric.

Actumnus is in need of a thorough taxonomic revision, and as part of this, it will be important to take into account the morphological and

behavioural apomorphies that have evolved in several species in relation to their association with coral. While this association has only been documented for three species thus far, *viz. A. antelmei*, *A. digitalis* and *A. setifer*, it can be expected that other species with similar mor-phology will also prove to inhabit corals. In particular, characters such as the short stout legs with the last pair folding into the deeply exca-vated posterolateral margins, and the powerful claw morphology that allows these crabs to abrade holes in the coral bases, must be of generic significance. In this context it seems likely that species such as *Actumnus elegans* De Man, 1888, *A. granotuberosus* Garth & Kim, 1983, *A. intermedius* Balss, 1922, *A. margarodes* MacGilchrist, 1905, and *A. similis* Takeda & Miyake, 1969, amongst others, will need to be transferred into one or more new genera.

BEHAVIOUR & ECOLOGY
PRESENCE OF *A. SETIFER* IN MORETON BAY

Prior to this study, Campbell & Stephenson (1970) reported a single specimen of *A. setifer* in a dredge sample from south of Peel Island. Our observations of *A. setifer* in Moreton Bay were made at Mud, Green, Coochiemudlo, Peel, Bird and Goat Islands, at Dunwich and Myora on North Stradbroke Island, and at Wellington Point and Scarborough on the mainland side of the Bay (Fig. 2). All of these sites represent coral reefs except for Dunwich and Myora, where there are extant coral communities, and Scarborough where no live corals were observed.

Searches were made using viewing buckets, manta tows, snorkelling, wading and obser-vations from a boat in < 1 m water depth.

A. setifer was most commonly found in colonies of *Favia speciosa*, the most common coral species in Moreton Bay, but also occurred in other massive corals (*Favia*, *Favites*, *Goniopora* and *Cyphastrea* sp.), both living and dead. *F. speciosa* has not previously been reported as having such a relationship with crabs. Coral use by *A. setifer* appeared to be roughly proportional to the coral species' relative abundance, although this relationship was not quantified. Other coral morphologies are found in Moreton Bay (eg. branching, tabulate, foliose, encrusting), however *Actumnus* crabs were never observed utilising
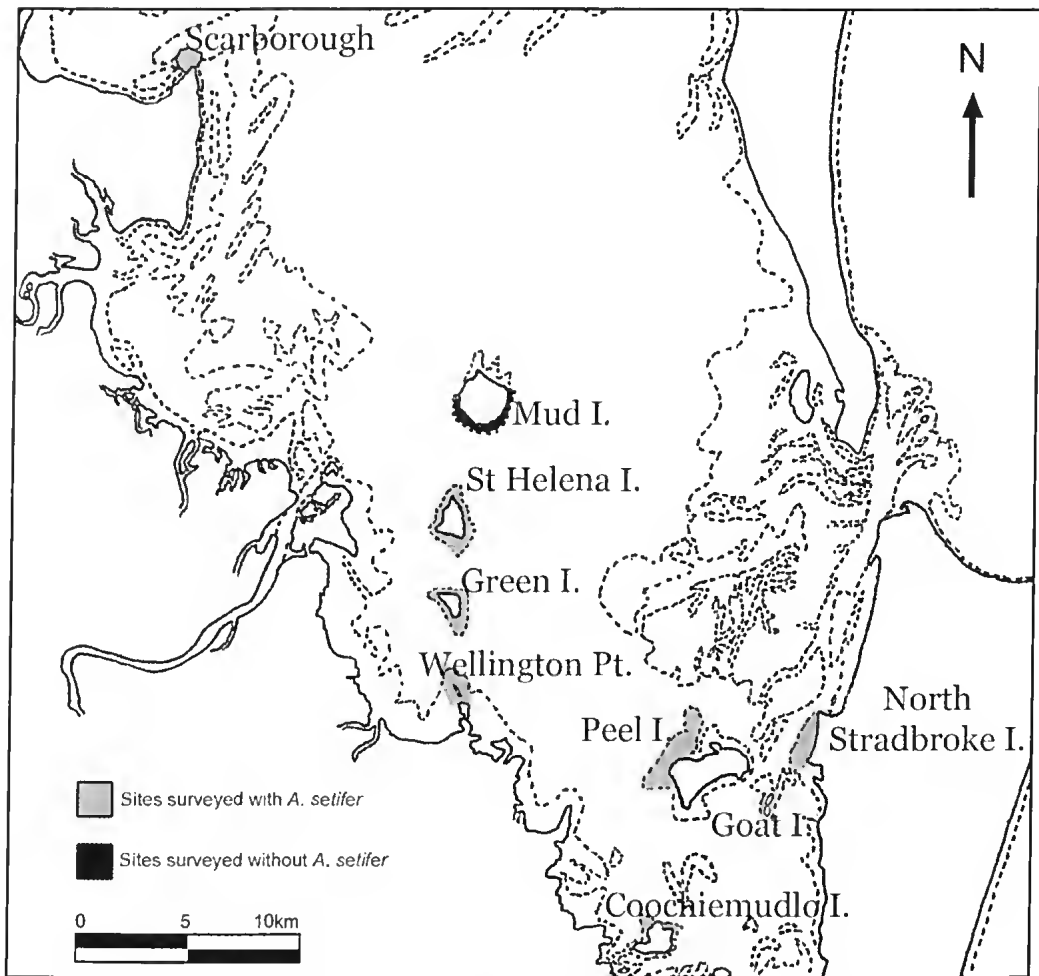
FIG. 2. Localities where coral-carrying *Actumnus setifer* have been observed in Moreton Bay.

coral colonies with morphologies other than massive.

A. setifer was predominantly found in areas of Moreton Bay proximal to living and dead coral reefs. The substrate in these areas was a sparse cover of massive corals and/or coral debris on patches of sandy or muddy sediments. These areas are consistent with the ecotone habitat of *Actumnus* crabs at Tutuila (Lamberts & Garth 1977). Areas of the Mud Island reef flat which were searched did not support the *A. setifer* coral association, while all other reefal areas searched did. Coral dredging of the Mud Island reef flat has created a substrate of loose rubble and steep slopes (Allingham & Neil 1995). This substrate would inhibit the movement of corals carried by crabs and also inhibit feeding by the

crabs, thereby excluding the *A. setifer* coral association from such sites.

BEHAVIOUR

Actumnus setifer observed in a salt water aquarium showed patterns of behaviour similar to those of the *Actumnus* crabs observed by Lamberts & Garth (1977). If the colony was overturned, the crab would roll it back so that the entrance to the burrow faced the substrate (see sequence of photographs in Fig. 3). Movement of the colonies was in small jerks, as the crab gripped the coral colony with the last pair of legs and pushed against the substrate with its chelipeds.

The burrows of *A. antelmei* and *A. digitalis* are excavated by the crab using the trabeculated manus of its chelipeds as a rasp (Ward 1942;
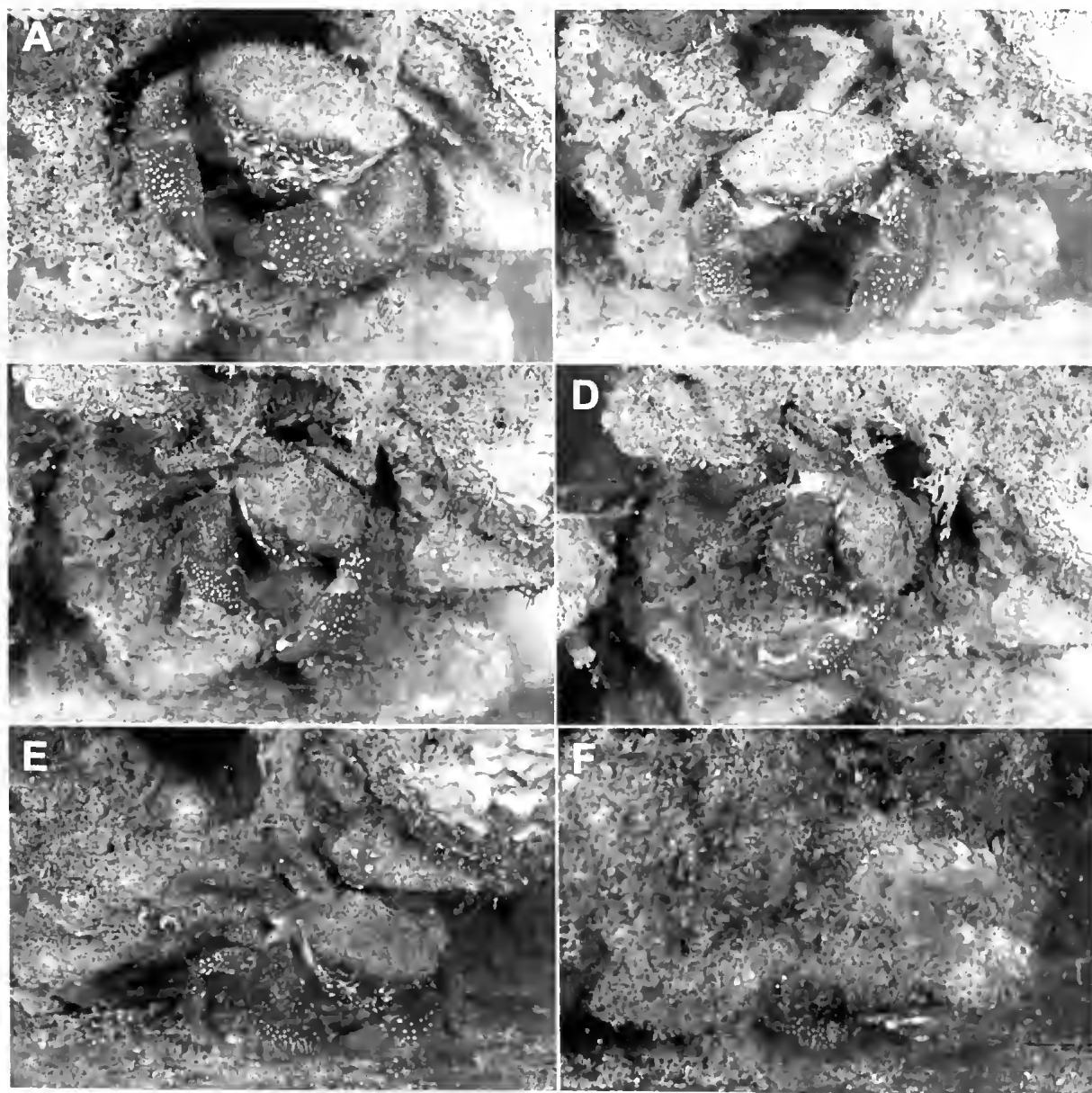
FIG. 3A–F. Sequence of pictures showing *Actumnus setifer* repositioning an upturned coral colony.

Lamberts & Garth 1977). This also seems to be true of *A. setifer*. Typical burrow morphology in a *Favia speciosa* colony consists of an entrance and feeding chamber on the underside of the colony (Figs 1E, 3, 4), a vertical shaft which opens to a habitation chamber, and small apertures to the upper (growth) surface of the coral colony. As many as 8–12 apertures may occur on a single colony 15–20 cm in diameter. Of 12 *A. setifer* inhabited colonies measured at

Green, Bird and Goat Islands wet weights ranged from 142g to 1106g, averaging 458g.

Crabs spent their time either at rest within the coral colony, feeding, or moving the colony. While at rest, crabs appeared to spend most of their time adjacent to the small apertures in the upper surface of the colony. This position is likely to facilitate respiration and detection of food. Feeding was usually undertaken in the large entrance chamber in the undersurface of

Massive Coral Colony (*Favia speciosa*)
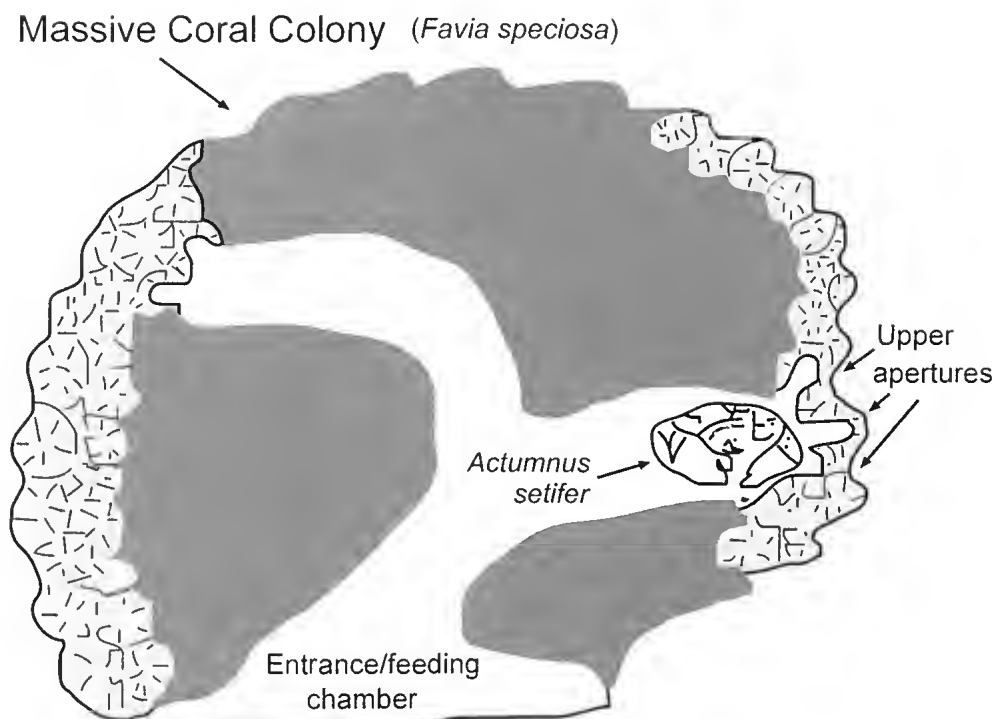
FIG. 4. Typical *Actumnus setifer* burrow morphology in a *Favia speciosa* colony.

the colony. Food was acquired by moving the colony over the top of the food, or occasionally by moving to the exterior of the colony and dragging the food item into the chamber. Even when obtaining food or righting the colony, crabs would seldom release their grip on the coral colony. This behaviour is identical for both sexes, and it would be interesting to know if female crabs release the first zoeae through the apertures in the upper surface, or whether they lift the colony clear of the substrate to facilitate more effective spawning.

SYMBIOSIS/MUTUALISM

While Lamberts & Garth (1977) and Marsh (1990) have referred to this type of coral-crab symbiosis as commensalism, we hesitate to use this term. Perhaps it is more a 'transportation mutualism' *sensu* Grutter & Irving (2007), similar to that of the Great Barrier Reef sipunculid *Aspidosi muelleri* that lives in a spiral cavity in solitary corals (Rice 1976). The sipunculid is protected under the coral which it moves around while it feeds, and the coral is kept upright on the substratum and transported to new feeding areas. This is essentially what Lamberts & Garth

(1977) suggested for the *Actumnus*/coral association. There is little formal evidence that transported corals have increased survival rates or growth benefits compared to attached corals, however one crab was observed to free itself, and the coral it lived in, from being completely buried in mud (I. Fellegara pers. observ.). Detrimental effects due to the presence of the crab have also been observed on a number of coral colonies. The formation of apertures requires the removal of some of the polyps and movement of the colony may result in tissue abrasion. Clearly this association is deserving of more study. As Grutter & Irving (2007) point out, 'positive interactions can play a fundamental role in maintaining the abundance and distribution of many marine species, as well as in structuring entire communities'.

CONCLUSION

Despite its widespread distribution throughout the Indo-West Pacific region and the general similarity of this distribution to that of hermatypic corals, *A. setifer* has not previously been reported as burrowing into, or carrying, coral

colonies. Similarly, although *F. speciosa* is also a widely distributed coral, overlapping in distribution with *A. setifer* throughout much of its range, no burrowing or carrying of this species by *Actumnus* crabs has been reported. An explanation for this lack of reporting may be that *Actumnus setifer* is locally less common in other areas, and because it is so well hidden within the coral clump, it has previously escaped attention. It may also simply be that because many small reef crabs, particularly those in the Pilumnidae and Xanthidae, occupy holes and crevices in rocks and coral, simply as places to hide, that the presence of *A. setifer* also in such shelters has been ignored as nothing unusual.

The central part of Moreton Bay appears to provide the perfect environment for this coral/crab association because of its low wave energy, numerous areas of sheltered coral patches dominated by small colonies of *Favia*, and the intervening areas of fine sediments with relatively little coarse coral debris. The *A. setifer/F. speciosa* association was found at every reef site which was searched with the exception of the dredged reef flat of Mud Island. The crabs absence at this site is attributed to the coral dredging method which left a residual deposit of mobile, coarse coral rubble covering the dredged substrate, thereby creating an unfavourable environment for these coral-carrying crabs.

ACKNOWLEDGEMENTS

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A comparison of coral composition on two artificial reef systems in Moreton Bay, southeast Queensland

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ABSTRACT

Artificial reefs are used for marine habitat rehabilitation in degraded ecosystems, and to help sustain local tourism activities such as the diving, snorkeling, and fishing. The artificial reefs of Amity Rockwall and Tangalooma Wrecks are widely used for recreational activities and have never been previously surveyed. These reefs are interesting because they are located between natural coral communities inside and outside Moreton Bay, and are intermediate in coral composition. A gradient in coral community composition has been previously reported with Faviidae dominating the coral communities inside Moreton Bay and Acroporidae more abundant at oceanic sites outside Moreton Bay. The study of these coral communities will help to understand the role of artifical reefs in Moreton Bay and how the coral communities change along a water quality gradient. ❑ *artificial reefs, corals, survey, distribution, habitat rehabilitation.*

The artificial reef of Tangalooma Wrecks is found on the western side of Moreton Island, 2 km north of the Tangalooma resort. The reef consists of 15 hulls scuttled along the shore for about 180 m from above the surface to about 8 m. The Department of Harbours and Marine commenced scuttling them to form a small craft anchorage in July 1963.

The artificial reef of Amity Rockwall was started during the 1970s and continues to be embellished to protect the township of Amity Point from erosion (Carter *et al.* 1994). The wall extends down to about 8 m to the sandy bottom, which continues further into the channel. Both artificial reefs are on the eastern side of Moreton Bay, in the proximity of the two major ocean exchanges, the South and North Passages, and receive clear oceanic water (Steele & Kuhl 1993; EHMP 2004).

MATERIALS AND METHODS

These artificial reefs were surveyed for the first time in May 2005 for scleractinian coral cover and species presence. Three 20 m point

FIG. 1. Tangalooma Wrecks, Moreton Island, Moreton Bay

FIG. 2. A large plate of *Acropora* coral on the Tanga-looma Wrecks. While the diversity is lower than at Amity, the colony size is larger.

intercept transects, recording coral presence/absence at 0.5 m intervals (Ohlhorst 1988), were carried out at Amity Rockwall and two tran-sects at Tangalooma Wrecks. The transects were carried out on snorkel at 1–2 m depth. A list of coral species was also compiled while swim-ming haphazardly.

RESULTS AND DISCUSSION

At Amity Rockwall, 27 species belonging to five families and 12 genera were recorded, and 19 species belonging to five families and nine genera were recorded at Tangalooma Wrecks (Table 1). *Acropora millepora, A. sarmentosa, Montipora peltiformis, Favites russelli* and *Acanthastrea regularis* from
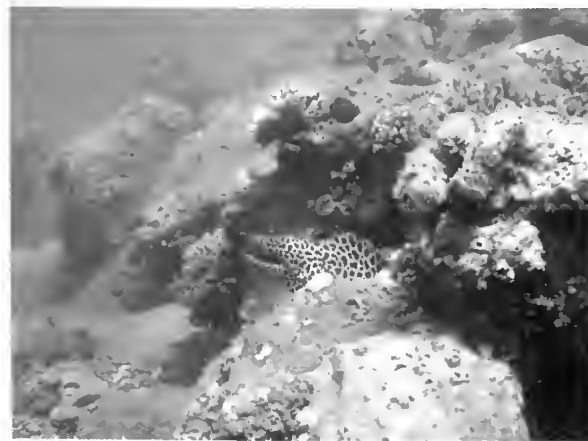
FIG. 3. Amity, Rockwall, North Stradbroke Island, Moreton Bay.

Amity Rockwall, and *Acropora samoensis, A. sarmentosa, Montipora faveolata, M. mollis, Leptoria* sp. and *Platygyra* sp. present at Tangalooma Wrecks were previously reported at Flinders Reef (Veron 1993), offshore to the north of Moreton Island, but have never been reported from the reefs inside Moreton Bay (Wells 1955; Lovell 1975, 1989; Harrison *et al.* 1991, 1995, 1998; Harrison & Veron 1993). These artificial reefs also create habitats for other marine creatures such as soft corals, and coral reef fish (pers. obs.).

The coral community of Amity Rockwall resembled the coral communites from the reefs inside and outside Moreton Bay with both Acropor-idae and Faviidae almost eqaully represented. The coral community of Tangalooma Wrecks had fewer species and resembled the coral communities from outside Moreton Bay, where *Acropora* spp. were more abundant. The differ-ence between in coral species present at the two artificial reefs may be due to their location: Amity Rockwall lies in the proximity of Peel and Goat Islands and may receive larval supply from there where Faviidae are more abundant, whereas Tangalooma Wrecks is relatively further away from the coral fringing coral reefs inside Moreton Bay and closer to Flinders Reef where Acroporidae are more common.

Tangalooma Wrecks had higher percentage coral cover (55.9 ± 10.71) than Amity Rockwall (23.57 ± 3.73). At Tangalooma Wrecks, some *Acropora* spp. colonies were over one meter in diameter, and minor damage was observed only on the corals growing on the external side of the wrecks. Coral colonies at Amity Rockwall were relatively smaller and extensive damage was observed caused by objects thrown to embellish the rockwall and by fishing lines. This suggests that Tangalooma Wrecks is less disturbed and corals growth is not impeded. Moreover, Tangalooma Wrecks is more strongly influenced by ocean water which is cooler in summer and warmer in winter (Lough 1994, EHMP 2004) allowing *Acropora* species colonies to grow relatively large.

Artificial reefs have been deployed in locations with different environmental conditions, from protected to open waters, and from clear to turbid waters (Rinkevich 2005; Shuhmaker 2002).

Table 1. List of scleractinian coral species observed during haphazard searches at the artificial reefs of Amity Rockwall (Am. Rk.) and Tangalooma Wrecks (Ta. Wr.) in Moreton Bay in May 2004.

Coral species	Am. Rk.	Ta. Wr.
ACROPORIDAE		
Acropora digitifera	√	√
A. divaricata	√	√
A. gemmifera	√	
A. glauca	√	√
A. hyacinthus		√
A. latistella		√
A. millepora	√	
A. nasnta	√	
A. samoensis		√
A. sarmentosa	√	√
A. solitaryensis	√	
A. valida		√
A. verweyi	√	
Montipora spp.		√
M. faveolata		√
M. mollis		√
M. peltiformis	√	
DENDROPHYLLIDAE		
Turbinaria frondens	√	
T. mesenterina	√	
T. peltata	√	
Barabattoia amicorum	√	
Cyphastrea serailia	√	
Favia matthai	√	
F. pallida	√	
F. rotumana		√
F. speciosa/favus	√	
Favites halicora	√	
F. russelli	√	
Goniastrea aspera	√	√
G. australensis	√	
Leptoria sp.		√
Montastrea curta	√	√
Platygyra sp.		√
MUSSIDAE		
Acanthastrea echinata		√
A. hemprichii	√	
A. regularis	√	
POCILLOPORIDAE		
Pocillopora damicornis	√	√
SIDERASTREIDAE		
Psammocora superficialis	√	√

The information gathered during this survey suggests that protected, well-flushed and shallow areas on the eastern side of Moreton Bay are better suitable for the recruitment of sessile invertebrates in general, and for scleractinian corals in particular. Further studies on organisms other than scleractinian corals, and on other artificial reefs in Moreton Bay (e.g. Curtin Artifical Reef), will help to understand the role of artificial reefs in Moreton Bay in creating new environments that can be used as a refuge by some organisms.

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Status of the subtropical scleractinian coral communities in the turbid environment of Moreton Bay, southeast Queensland

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ABSTRACT

The subtropical scleractinian coral communities of Moreton Bay exist in a marginal environment for reef corals. Moreton Bay is a shallow marine bay that is strongly influenced by adjacent rivers that discharge large volumes of freshwater, sediment and pollutants during periodic flood events. The 1974 flood caused catastrophic coral mortality at many sites in the western region of the Bay, while the 1956 flood caused heavy coral mortality on reefs around Peel Island. This paper provides a synthesis of the results of more recent quantitative surveys of the coral fauna and reefs during 1991, 1994, 2002 and 2003 to determine the status of the coral communities in Moreton Bay. Coral species richness and mean percentage coral cover increased at all sites surveyed in Moreton Bay after the 1974 flood, except along the eastern side of Green Island where coral cover remains less than 13% of the pre-flood cover. Mean live coral cover was highest at Myora Reef with 42–66%, and this is the only site within Moreton Bay that is dominated by *Acropora* corals. Mean coral cover at other sites ranged from 1–40% and the coral communities are dominated by massive corals, particularly brain corals from the Family Faviidae. A total of 63 scleractinian reef coral species from 21 genera from 10 families have now been recorded in Moreton Bay, which represents a substantial increase in coral species richness compared to the 18 coral species recorded prior to 1974. The re-zoning of the Moreton Bay Marine Park in 2008 provides an important opportunity to increase the protection of the unique coral communities in Moreton Bay. Based on these reef surveys we recommend increased protection for the reefs at southeast Peel Island and Goat Island because these sites contain high coral species richness, and the eastern reefs at Green Island because of the presence of large colonies of *Psammocora superficialis* dated at over 200 years old. ❑ *subtropical corals, high turbidity, flood impacts, coral resilience, marine park.*

Coral reefs are best developed in tropical regions where warm, clear and shallow seas provide abundant light, oceanic salinity and high aragonite saturation conditions suitable for reef-building by hermatypic scleractinian corals (Veron 2000; Harrison & Booth 2007). Substantial subtropical coral reefs also occur in some regions between latitudes 31°33′S and 33°48′N where warm tropical currents provide suitable conditions for reef accretion (e.g. Harriott *et al.* 1994, 1995; Veron 2000; Yamano *et al.* 2001; Harrison & Booth 2007). Where

Table 1. Mean percentage cover of scleractinian corals in Moreton Bay recorded by Lovell (1975) before the 1974 flood and the estimated percentage coral mortality after the flood. Mean percentage coral cover (± standard error) recorded after the flood by Lovell (1989), Harrison *et al.* (1991), Maguire (1994), the Environmental Protection Agency (EPA) (2004), and in 2002–03. - = no data.

Site	Pre-flood	Post-flood	Mortality	Source
Mud Is. SW	1	-	100	Lovell (1975)
Mud Is. S-SE	-	1.2 ± 0.3	-	2002
St Helena Is. S	1	-	100	Lovell (1975)
St Helena Is. S	-	13.8 ± 11	-	EPA (2004)
Green Is. W	4	-	100	Lovell (1975)
Green Is. W	-	0.8 ± 0.2	-	Harrison *et al.* (1991)
Green Is. W	-	8.9 ± 3.7	-	EPA (2004)
Green Is. E	36.2	-	70-90	Lovell (1975)
Green Is. E	-	1.8 ± 0.7	-	Harrison *et al.* (1991)
Green Is. E	-	4.6 ± 1.1	-	2002
Wellington Pt.	1.4	-	100	Lovell (1975)
Wellington Pt.	-	1.3 ± 0.8	-	Harrison *et al.* (1991)
Wellington Pt.	-	2.8 ± 1.6	-	2003
Empire Pt	2.8	1.2 ± 0.4	100	Lovell (1975)
Empite Pt.	-	1.2 ± 0.4	-	Harrison *et al.* (1991)
Empire Pt.	-	4.8 ± 0.9	-	2003
Coochiemudlo Is. N	1	-	100	Lovell (1975)
Coochiemudlo Is. N	-	6.1 ± 8.6	-	EPA (2004)
Peel Is. N-NE	12.3	-	0	Lovell (1975)
Peel Is. NE	-	17.9 ± 5.3	-	Harrison *et al.* (1991)
Peel Is. NE	-	36.6 ± 8.7	-	Maguire (1994)
Peel Is. NE		2.6 ± 1.4	-	Maguire (1994)
Peel Is. NW	-	17.9 ± 6.3	-	Maguire (1994)
Peel Is. N		9.8 ± 1.5	-	2002
Peel Is. SE	1	-	10	Lovell (1975)
Peel Is. SE	-	2.3 ± 0.7	-	Harrison *et al.* (1991)
Peel Is. SE	-	18.3 ± 8.6	-	Maguire (1994)
Peel Is. SE	-	6.9 ± 1.1	-	2002
Peel Is. SW	20.9	1.6	100	Lovell (1975)
Peel Is. SW	-	4.3 ± 1.3	-	Maguire (1994)
Peel Is. W	-	40.7 ± 3.7	-	EPA (2004)
Myora R.	1	-	0	Lovell (1975)
Myora R.	-	66.67 ± 9.8	-	EPA (2004)
Myora R.	-	42.3 ± 5.1	-	Harrison *et al.* (1991)
Myora R.	-	15 ± 4.9	-	2002
Bird and Goat Is. W	15.6	-	20	Lovell (1975)
Bird and Goat Is. E	5	-	10	Lovell (1975)
Bird and Goat Is. E	-	11.4 ± 3.6	-	Maguire (1994)

temperature and other environmental conditions become marginal or highly fluctuating for coral reef building, conditions have been described as marginal (sensu Kleypas *et al.* 1999) and non-reef building (Perry & Larcombe 2003). Some of these marginal coral communities have relatively high species diversity and coral cover (Harrison *et al.* 1991, 1998; Harriott *et al.* 1994, 1995; Riegl 1999; Perry & Larcombe 2003; Ferreira 2003). Moreton Bay is considered a marginal environment for scleractinian corals because of high turbidity and reduced light (Kleypas *et al.* 1999), however, some unique and thriving coral communities do exist in Moreton Bay and at Flinders Reef, to the north of Moreton Bay, where 40 and 119 coral species have been recorded respectively (Harrison *et al.* 1991, 1995, 1998).

Previous studies on the coral communities of Moreton Bay have indicated that floods are a major factor influencing their structure and ecology (Slack-Smith 1960; Lovell 1975, 1989). The impact of floods on the scleractinian corals of Moreton Bay was first documented by Slack-Smith (1960) who reported coral mortality between 0–10% and 100% on the northern and eastern reef flat of Peel Island after a heavy rainfall during the summer of 1956. During this event, *Favia speciosa* was the species mostly affected. Lovell (1975) also reported coral mortality up to 100% at most sites during the severe 1974 flood (Table 1). *Acropora, Goniopora, Turbinaria, Favia* and *Psammocora* present in Moreton Bay are, in decreasing order, negatively affected by flooding (Lovell 1989; Johnson & Neil 1988a). The coral community on the western reef of Peel Island, where coral death was estimated at 100%, was resurveyed in 1981 to assess coral recovery and 7 species of corals were recorded, 2 more than during the pre-flood period (Lovell 1989). Subsequent surveys on the coral communities in Moreton Bay were completed by Harrison *et al.* (1991) at Wellington Point, Empire Point and Green Island, by Harrison *et al.* (1995, 1998) at Myora Reef, by Maguire (1994) at Peel and Goat Islands, and by the Ecosystem Health Monitoring Program (EHMP 2004) at St. Helena Island, Green Island and along the western side of Peel Island.

Scleractinian coral communities in the vicinity of river systems are subject to coral mortality and loss of coral cover during periodic floods that cause reduced salinity, increased sedimentation and turbidity (McLaughlin *et al.* 2003; Restrepo *et al.* 2006). Coral mortality due to reduced salinity has been previously documented (e.g. Coles & Jokiel 1992; Morberg *et al.* 1997; Perry 2003), as well as the detrimental effects of increased sedimentation (Rogers 1990; Nugues & Roberts 2003; Fabricius 2005; Sanders & Baron-Szabo 2005) and nutrients on various aspects of coral physiology (Ward & Harrison 2000; Ferrier-Pagès *et al.* 2001; Harrison & Ward 2001; Koop *et al.* 2001; Cox & Ward 2002; Cruz-Piñón *et al.* 2003). Human activities including land clearing, agriculture practices and fishing resulting from the rapidly growing population of Brisbane directly affect Moreton Bay biota (Dennison & Abal 1999). Moreover, extreme temperatures, characteristic of a shallow bay like Moreton Bay, caused coral bleaching in Moreton Bay during the summer period in 1998 (I. Tibbetts pers. comm.).

The scleractinian corals of Moreton Bay grow on a late Holocene reef of unconsolidated fossil coral rubble mixed with terrigenous sediment (reviewed by Johnson & Neil 1998b). These subtropical coral communities are dominated by massive species, in particular by Faviidae, and certain unique assemblages of tropical, subtropical and temperate scleractinian species (Lovell 1975, 1989; Harrison *et al.* 1998). Wells (1955) recorded 24 species of scleractinian corals in Moreton Bay, whereas Lovell (1975) recorded 17 species. After the 1974 flood, Lovell (1989) reported the genus *Acanthastrea* for the first time in the Bay. Harrison *et al.* (1991) completed the most thorough taxonomic survey of scleractinian corals in Moreton Bay and recorded 40 species, 6 of which were new records for the Bay (Harrison & Veron 1993).

This paper presents a synthesis of recent surveys and data on the coral communities of Moreton Bay to assess their status. Changes in percentage coral cover, species richness, evenness and diversity over the period from 16–27 years after the 1974 flood are compared. These data provide a baseline for future surveys of the health of the coral communities in Moreton Bay and highlight important issues for the management of the Moreton Bay Marine Park.

Table 2. List of scleractinian coral species recorded at Myora Reef, in Moreton Bay, during surveys. * = Lovell (1975), ** = Harrison *et al.* (1995, 1998).

Coral species	1974*	1994**	2002
ACROPORIDAE			
Acropora sp.	x		
A. digitifera		x	x
A. divaricata			x
A. glauca			x
A. hyacinthus			x
A. latistella		x	x
A. loripes			x
A. lutkeni			x
A. solitaryensis		x	x
A. valida		x	x
A. verweyi		x	
POCILLOPORIDAE			
Pocillopora damicornis			x
SIDERASTREIDAE			
Coscinarea columna	x		
Psammocora superficialis		x	x
P. contigua	x		
MERULINIDAE			
Hydnophora exesa			x
DENDROPHYLLIDAE			
Turbinaria sp.		x	
T. peltata	x	x	x
MUSSIDAE			
Acanthastrea bowerbanki			x
A. echinata		x	
A. hemprichii			x
A. hillae		x	
A. lordhowensis		x	
FAVIIDAE			
Barabattoia amicorum		x	
Cyphastrea serailia		x	x
Favia maritima			x
F. matthaii			x
F. pallida			x
F. rotumana			x
F. speciosa-favus	x	x	x
Goniastrea aspera			x
G. australensis		x	
Leptastrea purpurea			x
Montastrea annuligera			x
M. curta			x
M. magnistellata		x	

Table 2 continued...

Coral species	1974*	1994**	2002
Oulophyllia crispa		x	
Plesiastrea versipora	x	x	
PORITIDAE			
Goniopora sp.		x	
G. djiboutiensis			x
PECTINIIDAE			
Echinophyllia aspera			x
Mycedium elephantotus	x		
Total no. of species	**7**	**19**	**27**

MATERIALS AND METHODS

FIELD SURVEYS

Extensive surveys of the coral and benthic communities were completed on the fringing reefs of Green Island, Wellington Point, Empire Point and Peel Island in May and June 1991 (Harrison *et al.* 1991). Quantitative surveys consisted of 32 line transects aligned perpendicular to the shore covering both intertidal and subtidal areas with a total of 18.8 km of transects. A total of 960 4 m² quadrats were examined at 20, 25 or 50 m intervals along the transects in the intertidal areas, and at 10, 20 and 25 m intervals in the subtidal areas. The identity, number and size of all scleractinian corals within the quadrats were recorded; together with percentage cover of soft corals, mussels, algae and seagrasses, and the type of substratum was recorded. In the lower intertidal area and in the subtidal areas, the line intercept length, identity and size of corals intercepting the transect tape were recorded. The coral species present within the vicinity of each transect and in haphazard searches at each site was noted, and specimens of any coral species requiring taxonomic verification were collected using a hammer and chisel, and placed in a coded plastic bag. These samples were subsequently labelled with a coded plastic tag attached with plastic-coated wire and then bleached in a concentrated sodium hypochlorite solution to remove the polyp tissues. The skeleton samples were identified according to the taxonomic classifications of Veron and Pichon (1976, 1980, 1982), Veron *et al.* (1977), Veron & Wallace (1984) and Veron (1986), and species identifications were confirmed by C. Wallace & J. Veron (see Harrison *et al.* 1991; Harrison & Veron 1993).

Table 3. List of scleractinian coral species observed at Peel Island, in Moreton Bay, during surveys. * = Lovell (1975, 1989), ** = Harrison *et al.* (1991).

Coral species	1974, 1989*	1991**	2002
ACROPORIDAE			
Acropora digitifera	x		x
A. divaricata			x
A. glauca			x
A. solitaryensis			x
A. verweyi		x	x
POCILLOPORIDAE			
Pocillopora damicornis			x
SIDERASTREIDAE			
Coscinarea columna	x		
Psammocora superficialis		x	x
P. contigua	x	x	
FUNGIIDAE			
Cycloseris cyclolites		x	
MERULINIDAE			
Hydnophora exesa	x		
DENDROPHYLLIDAE			
Turbinaria frondens	x	x	x
T. mesenterina			x
T. peltata	x	x	x
T. patula			x
T. radicalis			x
MUSSIDAE			
Acanthastrea sp.	x		
A. bowerbanki		x	x
A. echinata		x	x
A. hemprichii			x
A. lordhowensis		x	x
Blastomussa wellsi		x	
Lobophyllia hemprichii		x	
Micromussa amakusensis		x	x
FAVIIDAE			
Barabattoia amicorum		x	x
Cyphastrea serailia	x	x	x
Favia danae		x	x
F. lizardensis		x	x
F. maritima		x	x
F. matthaii		x	x
F. pallida		x	x
F. rotumana			x
F. speciosa-favus	x	x	x
F. stelligera	x		

Table 3 continued...

Coral species	1974, 1989*	1991**	2002
Favites abdita	x	x	
F. halicora	x		x
F. chinensis			x
F. complanata			x
F. flexuosa		x	x
Goniastrea aspera		x	x
G. australensis		x	x
Montastrea annuligera			x
M. curta		x	x
M. magnistellata		x	
Oulophyllia crispa		x	
Plesiastrea versipora	x	x	x
Platygyra lamellina	x	x	
PORITIDAE			
Goniopora columna			x
G. djiboutiensis		x	x
G. lobata	x		x
G. minor		x	x
G. stokesi			x
G. stutchburyi	x		x
PECTINIIDAE			
Echinophyllia aspera		x	x
Total no. of species	**16**	**32**	**42**

A total of 18 line transects were surveyed at Green Island, 14 of which continued across the subtidal region for up to 1 km for some transects. Eight intertidal and subtidal transects were surveyed at Wellington Point-Empire Point, and two at Peel Island, one transect near the Platypus wreck and the other east of the Lazaret Gutter. In addition, extensive visual surveys were done at Green and Peel Islands to identify any other coral species present (Harrison *et al.* 1991). In 1994, quantitative surveys were completed at Myora Reef at a depth of 1–3 m using five 50 m video transects oriented parallel to the reef edge within the main coral community (Harrison *et al.* 1995). Two sites were also surveyed approximately 30–50 m inshore from the main coral community using ten 1 x 1 m quadrats (Harrison *et al.* 1995, 1998).

Subsequent surveys were completed during 2002 at Mud Island, Green Island, Peel Island, and Myora Reef, and during 2003 at Wellington

Table 4. List of scleractinian coral species observed at Mud Island in Moreton Bay, during surveys. * = Lovell (1975).

Coral species	1974*	2002
ACROPORIDAE		
Acropora glauca		x
A. solitaryensis		x
DENDROPHYLLIDAE		
Turbinaria peltata	x	
FAVIIDAE		
Favia danae		x
F. maritima		x
F. matthaii		x
F. pallida		x
F. speciosa-favus	x	x
Goniastrea aspera		x
PORITIDAE		
Goniopora lobata	x	
G. stokesi		x
Total no. of species	**3**	**9**

Table 5. List of scleractinian coral species observed at Green Island, in Moreton Bay, during surveys. * = Lovell (1975), ** = Harrison *et al.* (1991).

Coral species	1974*	1991**	2002
ACROPORIDAE			
Acropora digitifera	x		
A. glauca			x
A. solitaryensis		x	
A. valida		x	
SIDERASTREIDAE			
Psammocora superficialis		x	x
P. profundacella			x
P. contigua	x	x	
PECTINIIDAE			
Mycedium elephantotus	x		
MERULINIDAE			
Hydnophora exesa	x		
DENDROPHYLLIDAE			
Turbinaria frondens	x		
T. peltata	x	x	x
MUSSIDAE			
Acanthastrea bowerbanki			x
A. echinata		x	x

Table 5 continued...

Coral species	1974*	1991**	2002
A. lordhowensis		x	x
Micromussa amakusensis		x	x
FAVIIDAE			
Barabattoia amicorum		x	
Cyphastrea serailia	x	x	x
Favia danae		x	
F. maritima		x	x
F. matthai		x	x
F. veroni			x
F. pallida		x	x
F. speciosa-favus	x	x	x
Favites abdita	x	x	x
F. halicora	x		
F. flexuosa			x
Goniastrea aspera		x	x
Plesiastrea versipora	x	x	x
Platygyra lamellina	x		
PORITIDAE			
Goniopora columna		x	x
G. djiboutiensis		x	x
G. lobata	x	x	x
G. minor		x	x
G. stokesi		x	x
G. somaliensis		x	x
G. stutchburyi	x	x	x
G. tenuidens		x	
Total no. of species	**14**	**26**	**25**

Point and Empire Point. At each site, 48 quadrats of 1 m² were surveyed. Eight quadrats were surveyed along each 20 m line transect with a total of three transects in shallow water (0.5–1 m below chart datum) and three transects in deeper water (2.5–3.5 m below chart datum). The transects were placed parallel to the shore and spaced 5 m from each other. Within each quadrat, each coral colony was identified to species level and its area measured to the nearest cm² by recording the longest diameter and the perpendicular diameter. At Myora Reef, six transects were surveyed within the area of the *Acropora* community, and six transects were surveyed outside the *Acropora*

Table 6. List of scleractinian coral species observed at Wellington and Empire Points, in Moreton Bay, during surveys. * = Lovell (1975), ** = Harrison *et al.* (1991).

Coral species	1974*	1991**	2003
ACROPORIDAE			
Acropora sp.			x
A. latistella		x	
SIDERASTREIDAE			
Psammocora superficialis		x	x
P. albopicta		x	
DENDROPHYLLIDAE			
Turbinaria mesenterina			x
T. peltata	x	x	
MUSSIDAE			
Acanthastrea bowerbanki		x	
A. echinata		x	x
A. lordhowensis		x	x
Micromussa amakusensis		x	
FAVIIDAE			
Barabattoia amicorum			x
Cyphastrea serailia	x	x	x
Favia danae		x	
F. maritima		x	x
F. pallida		x	
F. speciosa-favus	x	x	x
Favites abdita	x	x	
F. halicora	x		
F. flexuosa		x	
Goniastrea aspera		x	x
G. australensis		x	x
Plesiastrea versipora		x	x
PORITIDAE			
Goniopora djiboutiensis		x	x
G. columna			x
G. lobata	x	x	x
G. minor		x	x
G. stokesi		x	
G. somaliensis			x
G. stutchburyi		x	x
Total no. of species	**6**	**23**	**19**

area. In order to record all the coral species present at each site, haphazard searches were conducted for about an hour. Coral species lists were also compiled for Goat Island and Polka Point using haphazard searches, but coral cover was not quantified at these sites. Due to the difficulty in distinguishing between *Favia speciosa* from *Favia favus* in the field, these two species were grouped together for analysis as *Favia speciosa-favus*. For corals requiring taxonomic verification, skeleton samples were collected and identified as described above, with additional species information from Wallace (1999) & Veron (2000).

SPECIES RICHNESS, EVENNESS AND DIVERSITY INDICES

Species richness was calculated as the total number of species recorded within the quadrats along each transect. Brillouin's evenness (BE) and diversity index (HB) (Magurran 2004) were calculated in order to compare the 1991 and 2002 survey data. These indices were calculated on the number of individual colonies.

Brillouin diversity was calculated using:

$$HB = \frac{lnN! - \sum ln n_i!}{N}$$

Where n_i = the number of colonies of each species, and N = the total number of corals in the transect.

Brillouin evenness was calculated using:

$$BE = HB/HB_{max}$$

HB_{max} is given by:

$$HB_{max} = 1 / N \ln \frac{N!}{\{[N/S]!\}^{S-r} \{([N/S]+1)!\}^r}$$

where S = the total number of species, N = the total number of corals, $[N/S]$ = the integer of N/S, and $r = N-S[N/S]$. '!' = factorial.

To test for differences in species richness, diversity and evenness among locations and between the two time periods, a non-parametric Wilcoxon/ Kruskal-Wallis test was performed using JMP IN version 4.0.4.

RESULTS

PERCENT CORAL COVER

Coral cover showed a general increase from west to east within the bay. Mean coral cover ranged from 0.8% at Green Island west, to 42% at Myora Reef, recorded in 1991 and 1994, respectively (Table 1). There was a trend of

Table 7. List of scleractinian coral species observed at Goat Island and Polka Point, in Moreton Bay, during surveys. * = Lovell (1975, 1989), ** = Maguire (1994).

Coral species	Goat Is. 1974, 1989*	Goat Is. 1994**	Goat Is. 2003	Polka Pt. 2002
ACROPORIDAE				
Acropora sp.		x		x
A. digitifera	x		x	
A. divaricata			x	
A. gemmifera			x	
A. glauca			x	
A. loripes			x	
A. lutkeni			x	
A. solitaryensis			x	
Astreopora listeri			x	
SIDERASTREIDAE				
Psammocora profundacella			x	
P. contigua	x			
DENDROPHYLLIDAE				
Turbinaria sp.		x		
T. frondens			x	
T. mesenterina				x
T. peltata	x		x	x
T. patula			x	
T. radicalis			x	
MUSSIDAE				
Acanthastrea sp.		x		
A. bowerbanki			x	
A. echinata			x	
A. hemprichii			x	
A. hillae			x	
A. lordhowensis			x	
FAVIIDAE				
Cyphastrea sp.		x		
C. serailia	x			x
Favia sp.		x		
F. danae			x	x
F. maritima			x	x
F. rotumana				x
F. speciosa-favus	x		x	x
Favites sp.		x		
F. abdita	x			
F. halicora	x			
Goniastrea sp.		x		
G. aspera			x	x

Table 7 continued ...

Coral species	Goat Is. 1974, 1989*	Goat Is. 1994**	Goat Is. 2003	Polka Pt. 2002
Goniastrea australensis			x	
G. palauensis			x	
Montastrea curta			x	
Plesiastrea sp.		x		
P. versipora	x			
Platygyra lamellina	x			
PORITIDAE				
Goniopora djibutiensis			x	
G. lobata	x		x	
G. minor			x	
G. stokesi			x	
Total no. of species	**10**	**8**	**29**	**9**

increasing mean coral cover between the 1991–1994 and the 2002–2003 surveys at all locations (between 1 and 10%), except at the northern sites of Peel Island were mean coral cover decreased from 18% to 10%.

CORAL SPECIES AND SPECIES RICHNESS

During the 1991–1994 surveys, the total number of coral species recorded was 46, belonging to 19 genera from 8 families (Tables 2–7). During the 2002–2003 surveys the total number of coral species recorded was 51 belonging to 17 genera from 8 families. A combined total of 63 species were recorded during these combined survey periods, belonging to 21 genera from 10 families. *Favia speciosa-favus, Favia maritima* and *Goniastrea aspera* were the only species common at all locations. At Myora Reef, six species were present that were not observed elsewhere inside the bay: *Acropora hyacinthus, A. latistella, A. loripes, A. valida, A. verweyi,* and *Leptastrea purpurea. Astreopora listeri* and *Goniastrea palauensis* were only recorded at Goat Island. *Acropora gemmifera* was only observed at Goat Island. A total of 23 species were recorded in Moreton Bay that have not been recorded at Flinders Reef (Veron 1993): *Acropora loripes, Barabattoia amicorum, Blastomussa wellsi, Cycloseris cyclolites, Favia danae, F. lizardensis, F. matthaii, F. maxima, F. rotumana, F. stelligera, Favites halicora, F. complanata, Goniastrea aspera, G. palauensis, Goniopora columna, G. minor, G. stokesi, G. tenuideus, Leptastrea purpurea, Micromussa amakusensis, Oulophyllia crispa, Psammocora superficialis* and *P. albopicta* (Tables 2–7).

Coral species richness, evenness and diversity, recorded within the quadrats along the transects, all increased in more recent surveys compared with the study by Lovell (1975) (Table 8). The lowest species richness (5 species) was recorded at Mud Island and Empire Point during the 2002–2003 surveys. The highest species richness was recorded at the eastern side of Green Island (28 species) during the 1991 survey, but only 16 species were recorded at this site during the 2002 survey. Evenness was similar between the two survey periods at all locations except for Wellington Point, which was higher during the 2003 survey period (from 0.3–0.9). The lowest evenness was recorded at Wellington Point (0.3) and was relatively high at all other locations (0.6–0.9). The lowest coral species diversity was recorded at Mud Island and Myora Reef (0.5) during the 2002–2003 surveys. During both 1991 and 2002 survey periods, the highest coral species diversity was recorded at Peel Island south east (1.8). Species richness, diversity and evenness were all not significantly different between the survey periods in 1991–1994 and 2002–2003 (Wilkoxon/Kruskal-Wallis test: $p > 0.7$, $p > 0.5$ and $p > 0.1$, respectively).

DISCUSSION

The results of surveys in Moreton Bay over the past 16 years have shown a general increase in mean percentage coral cover since the study by Lovell (1975) and after the 1974 flood (Lovell 1989) at all sites, except at the eastern reef of Green Island. An increase in coral species rich-

Table 8. Coral species richness (total number of species found inside the quadrats along the transects). Brillouin diversity and evenness indices (mean ± standard deviation) calculated for the scleractinian corals of Moreton Bay by Lovell (1975) (*), Harrison *et al.* (1991) (**) and in 2002-2003 (***). - = no data.

Location	Richness	Diversity	Evenness
Mud Is SW*	3	-	-
Mud Is SW***	5	0.5 ± 0.3	0.8 ± 0.5
Green Is E*	14	0.3	0.4
Green Is E**	28	1 ± 0.5	0.8 ± 0.2
Green Is E***	16	1.2 ± 0.3	0.9 ± 0.1
Wellington Pt*	5	0.04	0.1
Wellington Pt**	24	0.7 ± 0.9	0.3 ± 0.5
Wellington Pt***	12	1.1 ± 0.2	0.9 ± 0.02
Empire Pt*	5	-	-
Empire Pt***	5	0.6 ± 0.4	0.6 ± 0.3
Peel Is SE*	5	0.3	0.5
Peel Is SE**	24	2.1	0.9 ± 0.04
Peel Is SE***	18	1.8 ± 0.3	0.8
Peel Is N*	9	0.2	0.2
Peel Is N**	21	1.6	0.7
Peel Is N***	19	1.3 ± 0.2	0.6 ± 0.1
Myora Reef*	5	-	-
Myora Reef**	11	-	-
Myora Reef***	11	0.5 ± 0.3	0.5 ± 0.4

ness was recorded at all sites. Myora Reef had the highest mean percentage coral cover but relatively low coral species richness, although a number of *Acropora* species were present only at that site.

CHANGES IN SCLERACTINIAN CORAL COMMUNITIES OVER TIME

The survey results showed some fluctuations in mean percentage coral cover over time. For example, there was a decrease in mean coral cover in 2002 at the northern reef of Peel Island since the study by Maguire (1994), and an increase at the western reef of Peel Island in 2002 (EHMP 2004) since the study by Maguire (1994). A considerable increase in mean coral cover was also recorded at St. Helena Island, Coochiemudlo Island, the western reef of Green and Peel Islands (EHMP 2004), and at the north east reef of Peel Island (Maguire 1994) since the study by Lovell (1975) and after the 1974 flood

(Lovell 1989). The increase in live coral cover and coral species richness recorded at most sites since the 1974 flood indicate that these coral communities are recovering. Variations in mean coral cover recorded at some sites during recent surveys may also reflect spatial patchiness and slight differences in the locations surveyed at each site. The mean percentage coral cover at S-SE Mud Island was low (1%) but similar to the pre-flood situation at SW Mud Island (Table 1). This was unexpected because at this location coral dredging occurred between 1937 and 1995 (Allingham & Neil 1995). This indicates either that some remnant corals survived the dredging, or that coral settlement and growth has been relatively high since dredging ceased. These communities have a very patchy distribution and although the variation in percentage coral cover may be due to differences in the locations sampled during each survey period, they indicate that coral cover is presently very low at Mud Island.

Under less disturbed conditions, the mean percentage coral cover has increased substantially at some sites in Moreton Bay (e.g. St. Helena Island, the western side of Green Island, the north-east side of Peel Island and Myora Reef, Table 1). The increase in coral cover is likely to result from growth of recruits at sites where coral mortality was very high following the 1974 flood, and at some sites from growth of surviving corals and more recent recruits. Lovell (1975) reports growth rates of *Favia speciosa* of approx. 0.5 cm in diameter per year. Roberts & Harriott (2003) reported similar growth rates for *Goniastrea australensis,* whereas *Cyphastrea serailia* grew faster and *Psammocora superficialis* grew more slowly. According to the measurements by Lovell (1975) coral colonies of 10 cm in diameter can grow 4 cm in eight years, which represents a 30% increase in size. However, distance from the mainland is likely to affect coral growth due to the gradient in water quality and environmental conditions (Johnson & Neil 1998b; Dennison & Abal 1999). Colony inversion can also substantially affect coral growth. Roberts (2000) observed frequent changes in growth trajectory and interruptions to colony growth caused by partial coral mortality. This process occurs typically in environments where

scleractinian corals grow on loose substratum, such as loose coral rubble that dominates most reefs in Moreton Bay, and colonies can easily been turned over by waves resulting in partial coral death and reduced growth. Boat anchors can also cause colony inversion, and may fragment corals. The presence or absence of suitable substratum for coral larvae (Harrison & Wallace 1990) is also likely to affect coral recruitment patterns within the bay (Harrison *et al.* 1998).

Since the 1974 flood, other stressors have acted upon these coral communities at different scales and have contributed to the different patterns of coral recovery or decline within the bay. These include the 1996 flood that caused increased sedimentation and pollutants within some parts of Moreton Bay. The adjacent city of Brisbane has one of the fastest growing populations in Australia (Skinner *et al.* 1998), and human activities such as land clearing and farming strongly interfere with Moreton Bay biota. Increased sedimentation, turbidity, nutrients and pollutants due to human activity have been long recognised as being detrimental to corals and affect their growth, survival and reproduction (Rogers 1990; Ward & Harrison 1997; Harrison & Ward 2001; Cruz-Pi ón *et al.* 2003; Sanders & Baron-Szabo 2005; Harrison & Booth 2007).

Due to the shallow nature of Moreton Bay, both extreme low and high temperatures occur occasionally (Johnson & Neill 1998b). Conspicuous coral bleaching has been observed in Moreton Bay in the summer of 1998 (l. Tibbetts pers. comm.) and winter and summer bleaching was observed during 2002 affecting some coral colonies at Green Island, Peel Island and Empire Point. This indicates that the minimum and maximum thermal tolerance limits for these corals are sometimes exceeded (Hoegh-Guldberg & Jones 1999).

SPECIES RICHNESS, EVENNESS AND DIVERSITY INDICES

Recent surveys have revealed a much higher number of scleractinian coral species compared to earlier studies by Wells (1955) and Lovell (1975, 1989). This may be partly due to recruitment by coral species new to Moreton Bay, but also due to improvements in taxonomic knowledge as new scleractinian species have been recognized (Harrison *et al.* 1991; Wallace 1999;

Veron 2000; Benzoni 2006). A re-examination of the coral reference collection at the Queensland Museum revealed that it contained a number of species not recognised at the time of the publication by Lovell (1975) (Wallace *et al.*, in prep.), and Benzoni (2006) described a new species, *P. albopicta*, which was collected at Wellington Point in 1991. Furthermore, rare species found at the limits of their distribution, can rapidly appear and disappear over time (Veron 1979; Harriott *et al.* 1995; Harrison & Booth 2007), and communities from locations where conditions are marginal are more easily subject to changes (Dollar & Tribble 1993; Glynn 2000). Bellwood & Hughes (2001) concluded that Acroporidae tend to become less common at sites with low species richness, whereas Faviidae become more common. The coral communities in Moreton Bay also reflect these trends as they have relatively low species richness and few Acroporidae, and tend to be dominated by Faviidae.

Evenness is inversely related to dominance, therefore maximum evenness (= 1) means that all species within an assemblage are equally abundant and that no species dominate (Magurran 2004). Evenness was relatively high at many locations suggesting that these coral communities are not dominated by any one species. In contrast, evenness was low at some sites where *Favia speciosa-favus* colonies were dominant (Table 8). During the 2002–2003 survey, 275 specimens of *F. speciosa-favus* were recorded from a total of 749 coral specimens (Fellegara, in prep.). Evenness was relatively low at Wellington Point in 1991 (Harrison *et al.* 1991) but showed a remarkable increase in 2003. This may be a consequence of a slight decrease in the number of species present (only 4) and an increase in mean percentage coral cover (from 1.3–2.8%) between the 1991 and the 2002 surveys. The main coral community at Myora Reef had an average diversity and evenness of 0.5. Although this community was dominated by *Acropora digitifera*, a number of other species represented by small colonies contributed to its higher diversity.

Most of the species found in Moreton Bay have a wide biogeographic distribution, such as *Plesiastrea versipora* and *Turbinaria frondens*, which occur as far south as Lord Howe Island and in some case as far south as southern

Australia (Veron 1993; Harriott *et al.* 1995; Veron 2000). A few of these species, such as *Acanthastrea hemprichii* and *Barabattoia amicorum*, are at the southern limit of their distribution (Veron 1993, 2000). *Pocillopora damicornis* occurs in a wide range of reef habitats and sometimes in mangrove wetlands (Veron 2000). However, although relatively common at Amity Rockwall and outside Moreton Bay at Flat and Shag Rocks (McMahon *et al.* 2002; Ford *et al.* 2003), only two live specimens of *Pocillopora damicornis* have been recorded within the Bay at Myora Reef and Peel Island, but none have been observed further inside the Bay during any surveys. A recent study on the identity of *Symbiodinium* dinoflagellate microalgae associated with the scleractinian corals and other symbiotic organisms present inside and outside Moreton Bay, showed that *P. damicornis* had different symbiont populations to all the other taxa examined inside Moreton Bay (Fellegara 2008). The *Symbiodinium* population found among the symbiotic organisms inside Moreton Bay was consistent across all organisms and showed very low diversity, which suggests that this specific *Symbiodinium* population is adapted to the subtropical and often turbid conditions in the Bay.

The *Acropora* species recorded in Moreton Bay have also a wide biogeographic distribution range, although *Acropora glauca* and *A. solitaryensis* are more commonly recorded at subtropical reefs south of the GBR (Wallace 1999). The *Acropora digitifera*-dominated community at Myora Reef supports a diversity of *Acropora* species that are not present further inside the Bay (Harrison *et al.* 1998). This may be due to the fact that Myora Reef receives clearer oceanic water twice a day, and it is therefore warmer in winter (Steele & Kuhl 1993; Harrison *et al.* 1995, 1998) and cooler in summer (EHMP 2004), compared to most other areas in Moreton Bay. This flux of oceanic water can also reach Peel Island within the bay and may have favoured the growth of some large colonies of *Acropora* cf. *solitaryensis*, up to approx. 2.5 m in diameter, on the submerged reefs along its northern side.

MANAGEMENT ISSUES

Most sites surveyed within Moreton Bay showed an increase in mean percentage coral cover, species richness, evenness and diversity since the 1974 flood. Some sites had considerably higher coral cover whereas at the eastern reefs of Green Island, coral cover was considerably lower than the pre-flood conditions. Green Island east is used both for commercial and recreational fishing; activities that increase pressure on this environment. Eastern Green Island used to have relatively high percentage of coral cover (34.2%, Lovell 1989) but the community has not recovered from the 1974 flood, hence protection of this site should be considered. This site is also important within Moreton Bay because of the presence of large *Psammocora superficialis* colonies (Harrison *et al.* 1991) that have been dated at over 200 years old (Roberts & Harriott 2003). These colonies create habitat complexity that favours the presence of commercial species, such as lobsters *Palinurus* sp., and reef fish species, such as the whiptail *Pentapodus setosus*, the knight fish *Cleidopus gloriamaris* and the moses perch *Lutjanus russelli*, which increase the biodiversity of Moreton Bay.

A higher level of protection of the reefs of SE Peel Island is recommended to conserve this area, as it has the highest coral richness and diversity recorded within Moreton Bay. Goat Island had a similar number of coral species to Peel Island and one species, *Astreopora listeri*, which has not been recorded elsewhere in Moreton Bay, although it has been reported at Flinders Reef (Veron 1993). A relatively large one-metre diameter colony of *Acropora gemmifera* was also observed at Goat Island. The reefs around Goat Island require a further and more detailed investigation to quantify the status of the coral community, the full coral species richness present, and to understand the effects of human activities, such as anchor damage from recreational fishing, and continuously resuspended sediment from increased ferry traffic near the island.

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Temperature control of burying and feeding activity of *Holothuria scabra* (Echinodermata: Holothuroidea)

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ABSTRACT

The relationships between temperature and burying and feeding behaviour of adult *Holothuria scabra* (sandfish) within a diel cycle was investigated. Animals were kept in aquaria in a constant light regime (14 h/10 h) and temperature was reduced 1°C each day from 24°C to 17°C. Burial state and behaviour (e.g. burying, feeding, resting) was scored at two-hourly intervals. Faeces were collected to investigate the relationship between sediment ingestion and temperature. A distinct diel burying and feeding cycle was exhibited, with most animals exposed and feeding between 13:00 and 20:00, and most buried and inactive between 01:00 and 09:00. Buried periods increased with decreasing temperature from 6.7 h per day at 24°C to 14.5 h per day at 17°C. Feeding activity decreased from 9.8 h a day at 24°C to 0.8 h per day at 17°C. A Generalized Linear Model showed temperature had a significant correlation with both feeding (p <0.001) and burying behaviour (p = 0.002). Faeces production also showed a statistically significant (p <0.001) relationship with temperature, and decreased from a daily production of about 40 g per day at 24°C to only 17 g per day at 17°C. Knowing when *H. scabra* will be buried is thus crucial for conducting visual population surveys for conservation and fishery research. Such surveys must have consistent diel and seasonal timing if results are to be meaningfully compared. In the southern hemisphere this would be during summer (December to February) from midday to late afternoon. ❑ *Holothuria scabra; burying; diel cycle; excretion rates; feeding; temperature; sea cucumber; sandfish*

Holothuria scabra Jaeger, 1833, commonly called sandfish, is one of the group of bottom dwelling holothurians. These species feed predominantly on bacteria and detritus by means of ingesting sediment and extracting organic material from it (Yingst 1976; Moriarty 1982; Baskar 1994; Conand 1999). *H. scabra* predominantly forages in the vicinity of seagrass beds, with shallow inshore waters being the preferred habitat and nursery area (Mercier *et al.* 2000a, b).

Holothuria scabra shows various cyclical patterns of burying depending on age (Yamanouchi 1939,

1956; Battaglene 1999; Mercier *et al.* 1999, 2000a; Uthicke 2001). Juveniles, probably due to their higher risk of predation, are synchronised by day/night regimes, burying at sunrise and re-emerging at sunset. When the juveniles reach about 40mm in length, they respond more to diel changes in temperature, by burying earlier at night (3:30) and emerging sooner during the day (12:00) (Mercier *et al.* 1999).

Studies on the burying activity of adult sandfish are scarce and fragmentary (Yamanouchi 1939, 1956; Skewes *et al.* 2000; Purcell & Kirby

2005). Yamanouchi (1939, 1956) studied *H. scabra* along with several other deposit-feeding species. However, his most detailed results about burying and feeding activity are in relation to `brown sandfish' (*Bohadschia marmorata*, then named *Holothuria vitiensis*) and he did not mention the effect of temperature on the animals. Skewes *et al.* (2000) studied *H. scabra in situ* on Warrior Reef, Torres Strait, during daylight hours and found that the animal's burying was cyclical and related to tides. However, sampling was done on only five occasions and results were highly variable depending on location and seagrass cover, and water temperature was not investigated. Purcell *et al.* (2005) were focused more on *in situ* locomotion than burying of *H. scabra*, and mentioned that adults bury during daylight only during the coldest period of the year. However, they did not specify at what temperature changes occurred.

Table 1. Glossary of terms used in this paper.

Term	Definition
activity	combination of burial state and behaviour of animal
activity cycle	diel (24 h) cycle of animal's activity pattern
activity of interest	2 feeding activities: not feeding and feeding
	3 burial states: buried, half-buried and exposed
resting	animal is inactive, meaning it has not moved for the last 5 minutes; this can occur whilst fully exposed, partially or fully buried
feeding	animal is actively feeding either on substrate or on walls; tentacles are exposed and head performs sweeping movements
burying/ emerging	animal is actively burying into or emerging out of the substrate
buried	animal is partially or fully buried into the substrate and inactive (see also 'resting')
burying cycle	diel (24 h) cycle of animal's burying pattern
excretion rate	rate at which animal excrete sediment (measured through dry weight of excreted sediment per 24 h)

Holothuria scabra's feeding activity can be somewhat independent of their burying cycle. Exposed animals are not necessarily feeding, while burying animals may still ingest sediment (Yamanouchi 1939, 1956; Wiedemeyer 1992; Mercier *et al.* 1999). While there are some conflicting reports in regards to the periodicity of feeding when the animals are exposed (Yamanouchi 1939, 1956; Wiedemeyer 1992; Mercier *et al.* 1999), authors agree on feeding cycles being pulsed and variable (Hamel *et al.* 2001; Purcell 2004), with some studies indicating temperature as a cue for certain feeding habits (Roberts *et al.* 2000). However, no study has investigated the relationship between temperature and feeding rates for adult *H. scabra*.

When addressing conservation and fishery management of *H. scabra*, an understanding of burying activity is crucial to minimise errors in population and distribution surveys. Additionally, seasonal variation in burying and feeding activity may affect ecosystem function and bioturbation rates attributed to holothurians within their habitat. The aim of this study was to investigate a possible relationship between burying/feeding activity and temperature, while excluding other possible factors that may influence the animal's burying and feeding pattern such as tides, current and light. The present study solely investigated burying and feeding behaviour under a decreasing temperature regime such as the animals might experience in the wild as autumn changes to winter.

MATERIALS AND METHODS

A glossary of terms used throughout this paper is presented in Table 1.

EXPERIMENTAL SET-UP

The experiment was carried out in a temperature controlled room at the Moreton Bay Research Station on North Stradbroke Island, Queensland.

Six aquaria were set up, each with 10 cm of muddy sand as the substrate. Based on results from previous studies and personal observations (Wiedemeyer 1992; Wolkenhauer unpub. data) this is an adequate sediment depth to allow for normal burying behaviour of adult *H. scabra*, since their anus is usually in constant contact with the water column to facilitate respiration.

Table 2. Activity of *H. scabra* in aquaria classed as combinations of burial state and behaviour.

Behaviour burial state	Fully buried	Half buried	Fully exposed
resting	1	2	3
burying		4	
emerging		5	
feeding levelled (on substrate)			6
feeding upright (on walls)			7
searching			8

The substrate was collected from the field at a shallow station where *H. scabra* is frequently visible (Myora Gutter, 27°27.876′S, 153°25.146′E). The sediment was neither sieved nor treated to keep natural food sources (micro flora and fauna) intact. Aquaria were filled with seawater and aerated.

Three artificial lamps (DegenPai 36W ATT BR-HG (UV bulb) and DegenPai 36W D-HG FL6500KT8 (daylight bulb)) were placed over the aquaria, each covering two aquaria to simulate natural summer light regimes (14 h light and 10 h darkness). At 10 cm water depth the light reading was 1200 lux or 100 fc, at 30 cm water depth (sediment-water interface) it was 450 lux or 36 fc. Temperature was set to 24°C. Each of the six aquaria was stocked with one adult sandfish (~17 cm length; ~300 g wet weight) collected from the above field location. The animals were left to acclimatise in the aquaria for two days before the experiment. Subsequently, temperature was decreased one degree every day for a week until reaching 17°C at the end of the experiment.

In addition, another 12 aquaria were set up in a wet laboratory as control animals for faeces collection in the same way as described above. The only difference to the aquaria set-up in the controlled room was ambient light (through ceiling flood lights and windows), and flow-through sea water at a constant ambient temperature of 24°C. The sampling design and data collection for ingestion rates of these animals was the same as the ones in the temperature controlled room and is described below.

SAMPLING DESIGN AND DATA RECORDING

We monitored aquaria every two hours for seven days and classified activity of the animals on each occasion as various combinations of burial state and behaviour (Table 2). Furthermore, faeces produced by each individual were collected two-hourly and weighed after each 24-hour period.

Two common activities of interest were established for the analysis of burying cycles: A) buried (score 1, 2, 4 and 5); and, B) exposed (score 3, 6, 7 and 8).

For the analysis of feeding activity, two activities of interest were also established: A) not feeding (score 1, 2, 3, 4, 5 and 8); and, B) feeding (score 6 and 7). We did not observe *H. scabra* ingest any sediment while stationary or searching, since oral tentacles were retracted, and these were considered resting/searching periods (score 3 or 8). Thus, only hours spent by the animals moving along the substrate/walls with oral tentacles extended were considered as feeding periods (score 6 and 7).

Two main approaches were used to characterise both burial state and feeding activity: i) the time of day of each animal's state within the diel cycle; and, ii) the average amount of time per day the animals spent in each state.

STATISTICS

Statistical analyses were done using R 2.5.0. In order to prepare the data for statistical analysis, we converted scores of different activities of interest into binomial form (true/false) and analysed the responses using a Generalized Linear Model (GLM) with binomial error structure. Each state, e.g. feeding/not feeding or buried/not buried, was therefore treated as a binary response and the probability of this behaviour occurring was estimated as a probability between 0 and 1. Furthermore, harmonic transformation of the time-of-day using sine and cosine functions, representing the daily feeding and burying cycles, were used as supplementary explanatory variables. A linear regression was used to analyse the correlation between temperature and excretion rates.
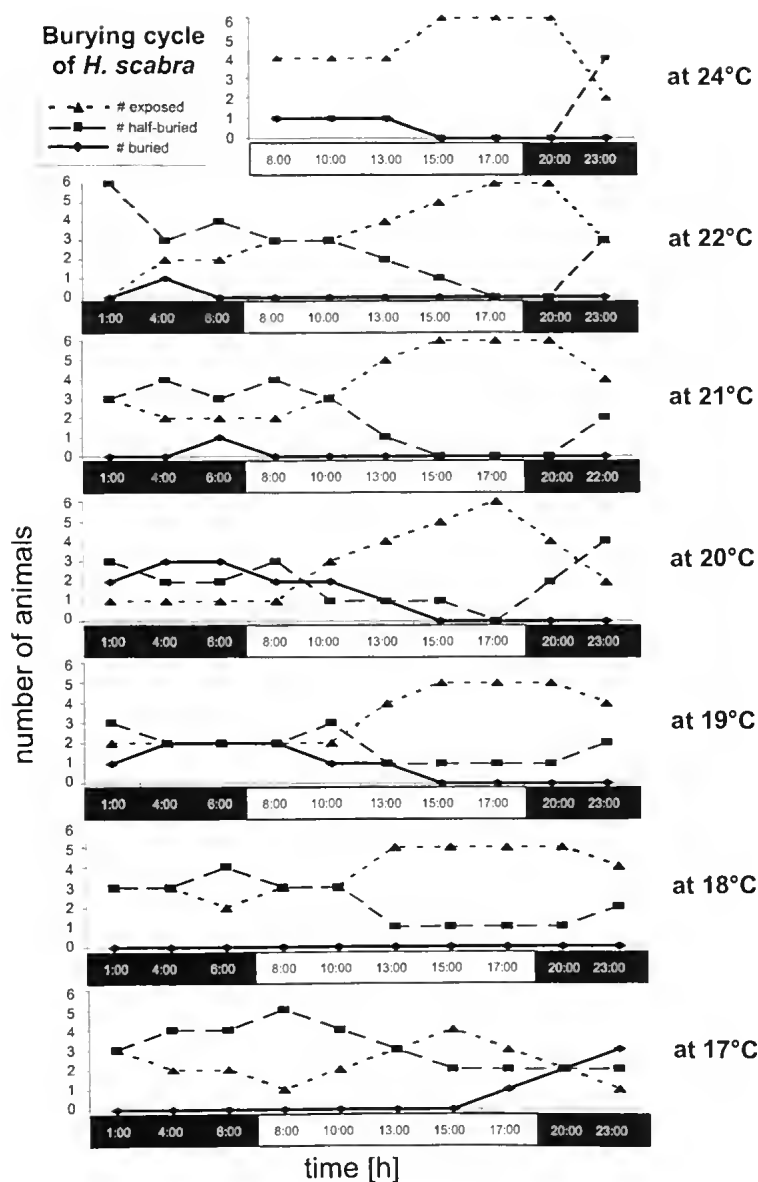
FIG. 1. Diel burying cycle of *H. scabra* with decreasing temperature. Open and solid bars on X-axis represent light and darkness.

RESULTS

TEMPERATURE EFFECTS ON BURIAL STATE

Holothuria scabra showed a distinct diel burying cycle (Fig. 1), with most of the animals exposed and active between the hours of 13:00 and 22:00 and most buried and inactive between the hours of 01:00 and 09:00. As experimental temperatures decreased, fewer animals spent time exposed and active, while more remained buried or half buried (Fig. 1). However, the trend of burying during the day did not change as such, but rather the burial duration lengthened.

The number of animals being buried (combining partially and fully buried) showed a significant (p = 0.002) negative correlation with
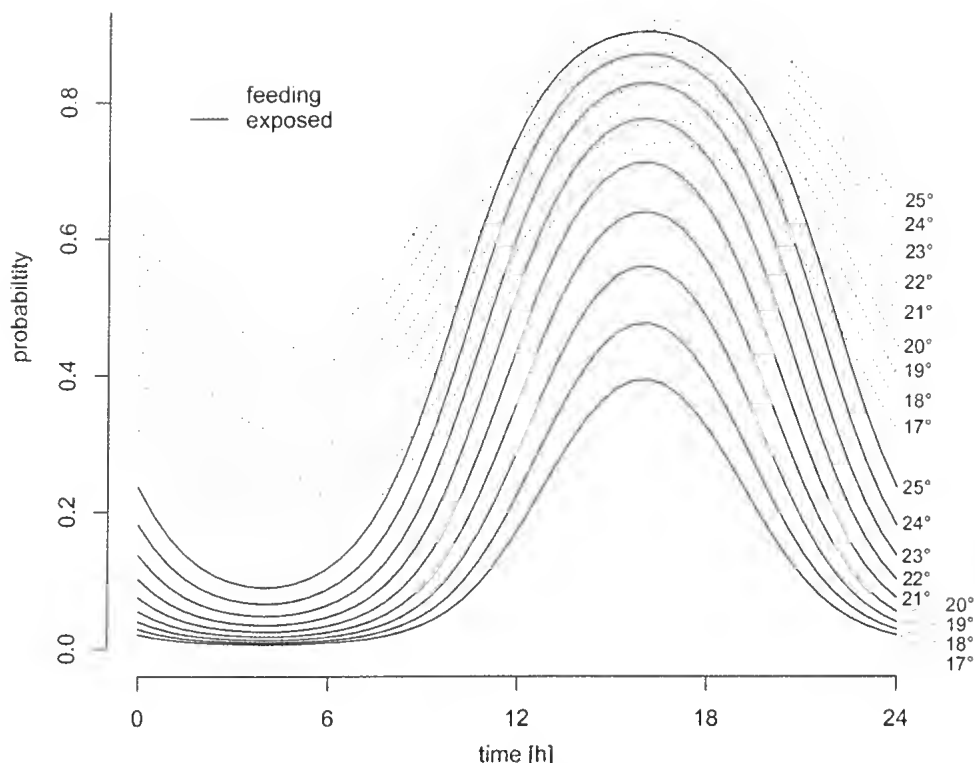
FIG. 2. Generalized Linear Model prediction of probability of feeding and burying behaviour (cos-sin function). Dotted line = probability of animals feeding, solid line = probability of animals being exposed. Numbers on the right represent the temperature in degrees celsius for each line.

temperature (Fig. 2, Table 3A). There was at least some period with the temperature above 20°C when no animals were buried, but a minimum of two out of six animals were buried at 17°C (Fig. 1). This effect was particularly obvious in the morning (08:00–10:00), with only one animal out of six being buried at 24°C, compared to four out of six animals being buried when temperature reached 17°C (Fig. 1).

Holothuria scabra's average duration of being buried increased with decreasing temperature (Fig. 3A). When comparing combined values of being buried (fully and partially) against being exposed, periods being buried increased from 6.7 h at 24°C to 14.5 h at 17°C within 24 h.

TEMPERATURE EFFECTS ON FEEDING ACTIVITY

There was a significant (p <0.001) correlation of feeding activity with temperature (Fig. 3B, Table 3B). Daily periods of feeding decreased by 9 h from 9.8 h at 24°C to about 0.8 h at 17°C. Especially during the last two days when temp-

erature fell from 18°C to 17°C, a strong decrease in feeding activity was noticeable which might indicate a threshold temperature.

TEMPERATURE EFFECTS ON FAECES PRODUCTION

Average daily faeces production decreased with decreasing temperature (Fig. 4), which formed a significant linear relationship (r^2 = 0.82, p <0.001, Table 4). The regression analysis indicated that there would be 5.7 g dry weight (DW) increase of faeces production with every degree of temperature up to 22°C. We also plotted the average faeces production from the twelve animals kept at a constant 24°C in flow-through aquaria. When we included data from two other studies, all results were close to the predicted regression line (Fig. 4).

DISCUSSION

BURYING CYCLES

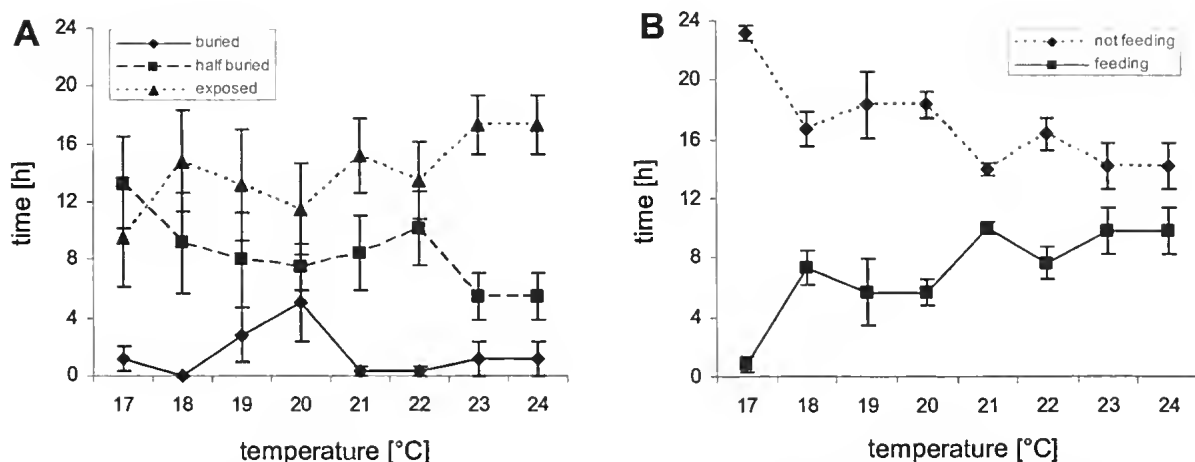This study shows that adult *Holothuria scabra* have a diel burying cycle as described for juv-

FIG. 3. Burying and feeding activity of *H. scabra* depending on temperature. **A.** Buried/half-buried versus exposed periods expressed as average hours spent in a day. **B.** Non-feeding versus feeding periods expressed as average hours spent in a day; error bars = 1 SE with n=6.

eniles (Battaglene *et al.* 1999; Mercier *et al.* 1999). Furthermore, the length of time spent buried shows a significant relationship to temperature. Purcell & Kirby (2005) also found more adult sandfish buried for longer periods during the day with decreasing water temperature. However, they did not specify any temperature range and did not investigate actual timeframes of the animals being buried based on a 24 hour-cycle since the observations took place only during daylight hours. Mercier *et al.* (2000a) found most adult *H. scabra* on the surface did not follow their usual burying cycle when water temperature increased to more than 30°C.

There are other known factors that cause sandfish to bury for prolonged periods of time such as stress (Purcell *et al.* 2006), spring tides and strong current (Skewes *et al.* 2000), predation (Dance *et al.* 2003) and desiccation or changes in salinity (Mercier *et al.* 2000a). These factors might counteract or prolong the effect temperature has on their burying cycle in the

Table 3A. Results of GLM analyses of burial state (exposed/not exposed) in relation to temperature.

Effect	Estimate	Standard error	z value	Pr (>|z|)
intercept	-3.270	1.172	-2.791	0.005
sin (t)	-1.266	0.162	-7.802	<0.000
cos (t)	-0.462	0.153	-3.027	0.003
temperature	0.175	0.057	3.075	0.002

Table 3B. Results of GLM analyses of feeding activity (feeding/not feeding) in relation to temperature.

Effect	Estimate	Standard error	z value	Pr (>|z|)
intercept	-8.402	1.597	-5.263	<0.000
sin (t)	-1.977	0.230	-8.602	<0.000
cos (t)	-1.139	0.207	-5.502	<0.000
temperature	0.335	0.075	4.452	<0.000

Table 4. Results of regression analyses of faeces production in relation to temperature.

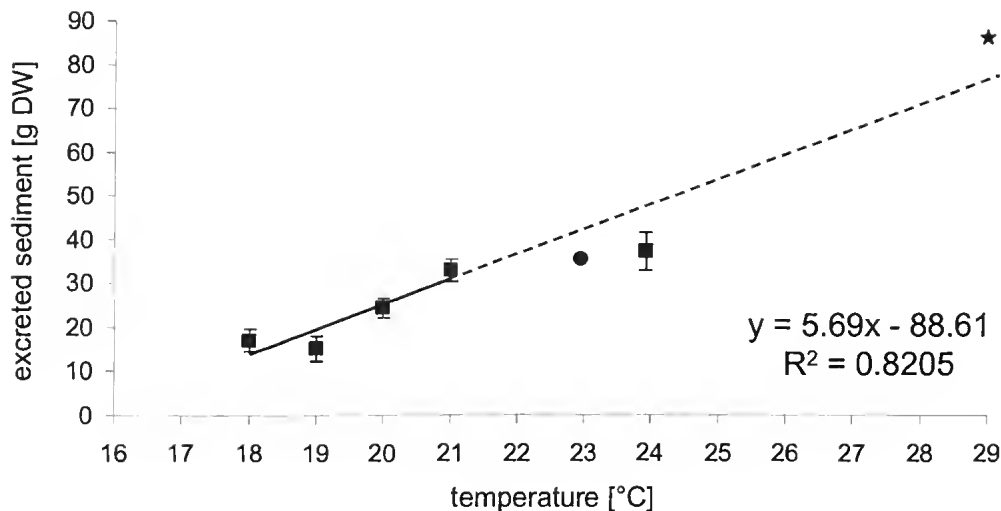| Effect	Coefficient	Standard error	t	P
intercept (constant)	-88.611	23.973	-3.696	0.001
temperature	5.693	1.227	4.638	<0.000

FIG. 4. Solid line shows regression of faeces production of adult *H. scabra* (expressed in gram dry weight) versus temperature per 24-hour period. Error bars = 1 SE with n=6, d.f.=22. Dotted line is an extrapolation based on solid line. Three data points are added from other studies (but not included into analysis). Square represents 39.2 g faeces production at 24°C (control animals in this study), dot represents 38.4 g faeces production at 23°C (Purcell 2004) and star represents 88.8 g faeces production at 29°C (Mercier *et al.* 1999).

wild. However, this study aimed specifically to exclude those variable factors to find a potential underlying pattern in response to temperature alone.

Further study is needed to determine how light and temperature interact and if adult *H. scabra* have a potential tendency to reverse their burying cycle in accordance with reversed light regimes, overruling the temperature effect, as has been shown for smaller juveniles (Mercier *et al.* 1999).

FEEDING CYCLES

Decreasing temperature has a significant effect on the animal's time spent exposed and feeding. The significant decrease in feeding behaviour between 18°C and 17°C (Bonferoni pair-wise comparison, p <0.001) supports a potential threshold temperature at 18°C for *H. scabra*. This is the usual winter minimum in Moreton Bay and sandfish do not occur any further south than this estuary (see distribution in Hamel *et al.* 2001), suggesting its southern distribution is temperature limited.

Studies on feeding behaviour of other echinoderms show similar effects with temperature (Schinner 1993; Hollertz & Duchêne 2001; Thompson & Riddle 2005). For example, Thompson &

Riddle (2005) showed that the sea urchin *Abatus ingens* increased its displacement activity with increasing temperature.

EXCRETION RATES

In the present study we show that the amount of faeces excreted by *H. scabra* has a significant positive relationship to temperature, and that our average excretion rate (33 g per 24-hour period at 22°C) correlates well with other studies (Mercier *et al.* 1999; Purcell 2004). Studies on ingestion rates of other echinoderms showed similar responses to decreasing temperature. For example, the heart urchin *Brissopsis lyrifera* decreased its ingestion rates from 1.92 g to 0.48 g dry sediment day^{-1} when kept at 13°C and 7°C, respectively (Hollertz & Duchêne 2001).

Further investigation at higher temperatures is needed before a potential peak efficiency for food ingestion in relation to temperature can be estimated. *H. scabra* is a tropical species attaining its best growth rate and reproduction at water temperature ranging from 25–30°C (Hamel *et al.* 2001).

CONCLUSION

Our data indicate that observed differences in burying and feeding behaviour of adult *Holothuria scabra* are strongly related to changes

in water temperature. These findings have implications for population surveys for this species, and related holothurians, when relying on visually counting animals during distribution and abundance surveys. Surveys should be conducted at consistent diel and seasonal timing if results are to be compared with previous data. Based on burying data presented here, we suggest the most suitable time to conduct population surveys on *H. scabra* would be during summer from midday to late afternoon. A reduction in ingestion rates at lower temperatures also indicates that bioturbation does not occur at equal rates during the year. Hence, the ecosystem function of holothurians is altered dependent on seasons and this needs to be taken into account when evaluating the ecological function of these animals within their habitat.

ACKNOWLEDGEMENTS

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Biology of the swash-riding Moon Snail *Polinices incei* (Gastropoda: Naticidae) predating the Pipi, *Donax deltoides* (Bivalvia: Donacidae), on wave-exposed sandy beaches of North Stradbroke Island, Queensland, Australia

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ABSTRACT

On the highly exposed sandy shores of the eastern coast of North Stradbroke Island, Queensland, and on One Mile Beach, further south at Port Stephens, New South Wales, the naticid moon shell *Polinices incei* surfs up the beach to attack juvenile surf clams, or pipis, (*Donax deltoides*). It moves shallowly within the sand, its presence indicated by a raised trail. Apparently, the surf clams recognise *P. incei* in their vicinity as they, unusually, emerge from the sand and attempt to escape from the predator by leaping. If captured, however, surf clam juveniles (up to three individuals) are held by *P. incei* beneath the posterior margin of its foot. *Polinices incei* was also recorded drilling *D. deltoides* lower down the shore.

To move up shore and return down shore, *Polinices incei* 'surfs' the swash and back-wash, respectively. Surfing involves rapid inflation of the foot and propodium such that the predator floats shell down but is carried by the waves either up or down. Surfing downshore, *P. incei* was often observed holding bivalve prey. Downward migrating *P. incei* individuals also 'roll' in the backwash, but brake by digging in the anterior end of the foot and resume burrowing rapidly. Other identified behaviours include hunting and galloping — the latter to chase potential prey.

The nassariid *Bullia digitata* surfs similar exposed beaches in South Africa, but to access carrion. As far as is known, therefore, *Polinices incei* is the only known naticid predator which has evolved a surfing behaviour that enables it to attack its prey, the tidally migrating surf clam *Donax deltoides*. The evolution of naticid drilling predation is part of the Mesozoic Marine Revolution. As predicted by escalation theory, the dangers to infaunal bivalve residents from naticid predation seem to have increased over time but since shallow water benthic assemblages are thought to be particularly susceptible to mass extinction events it seems probable that the *Polinices incei* (predator)/*Donax deltoides* (prey) relationship is relatively modern. Hitherto, surf clams have always been regarded as occupying a 'safe refuge' niche, at least from marine predators. The relationship identified herein, therefore, is a remarkable example of predatory adaptive radiation. ❑ *exposed sand beaches, eastern Australia, Polinices incei, Naticidae, Donax deltoides, Donacidae, surf clams, swash riding, predation.*

Virtually worldwide on beaches of sand and mud, and offshore on similar sediments, species of the mesogastropod Naticidae are predators of resident bivalves. This has been reviewed most recently by Kelley & Hansen (2003), especially with regard to the fossil record of drilling predation. Naticids can be traced back to the early Jurassic, some 200 million years ago (Taylor 1981), and representative species thus constitute some of the earliest drilling molluscan predators. Prey can include foraminiferans, and other gastropods but, more usually, bivalves. Naticids typically drill a characteristic countersunk borehole through the bivalve shell, using a combination of mechanical drilling using the radula, and chemical etching by secretions from an accessory boring organ (ABO) in the mouth to penetrate the shell of the prey (Carriker 1981). Drill holes are made usually on the dorsal valve surface, often above the nutritious visceral mass (Negus 1975), or, in the case of the tropical *Polinices* species, at the valve margin (Vermeij 1980; Ansell & Morton 1985, 1987).

Intertidal naticids are typically inhabitants of relatively sheltered beaches, and attack their prey underground. In subtropical Hong Kong such sheltered beaches often possess a suite of naticids that partition the bivalve resources of their habitat (Ansell & Morton 1985), typically in relation to shell thickness. Similarly, Morton & Knapp (2004) have shown that in the warm, shallow waters off Florida, *Naticarius canrena* (Linnaeus, 1758) feeds on a wide variety of bivalve prey but notably *Chione elevata* (Say, 1822). In more temperate waters, resident naticids have a more conservative diet. Wiltse (1980) demonstrated that the larvae of *Polinices duplicatus* (Say, 1822) settle in close proximity to populations of its sole bivalve prey *Gemma gemma* (Totten, 1834). There is a large literature on naticids and the biology of their predatory behaviours (Kabat 1990).

Because they are thought to track their prey underground using olfactory cues, naticids are typically absent from high-energy, wave disturbed, beaches although, as this study will demonstrate, one species of naticid in eastern Australia is an exception to this generalisation.

Ansell & Trevallion (1969) point out that macrobenthic species that live in constantly disturbed high-energy sandy substrata, have evolved specific morphological and, equally important behavioural features to allow them to flourish. Some species that can exploit such habitats are called 'swash riders', because of their ability to exploit the force of waves racing up the shore. Such species must also exploit the backwash, typically on the falling tide, to escape the dangers of desiccation. Species of the tropical Donacidae surf clams (Bivalvia) are well known to exploit the swash and the backwash to keep within the zone of breaking waves in order to feed on the sparse nutrients held briefly in suspension by them (Ansell 1981). Similarly, there are several swash-riding species of *Bullia* that occur in South America, south and west Africa, and the Indian Ocean (Brown 1982). Most notably, *Bullia digitalis* (Dillwyn, 1817) periodically expands its foot and uses it like a sail to be propelled upwards by the swash (Brown 1961, 1971, 1979; Ansell & Trevallion 1969). *Bullia* species, including *B. digitalis*, have been reported to ride the swash on South African surf beaches (Odendaal *et al.* 1992) although this is to seek carrion food rather than live prey (Hodgson & Brown 1987). Brown *et al.* (1989) have reviewed the similarities and differences between bivalves (*Donax serra* (Röding, 1798)) and gastropods (*B. digitalis*) that occupy wave-exposed sandy beaches in South Africa.

On West Malaysian shores, the highly active, filter feeding trochid *Umbonium vestiarium* (Linnaeus, 1758) is the sole prey of *Natica maculosa* Lamarck, 1822 (Berry 1982). In the Azores, huge numbers of drilled tellinids, *Ervilia castanea* (Montagu, 1803), wash up on wave-exposed beaches, where it was once believed they had been attacked by the naticid *Natica* cf. *intricata* (Donovan, 1804). However, Morton (1990a) has shown that *E. castanea* actually lives subtidally (to depths of ~50m), and neither it nor its predator occurs intertidally.

Polinices incei (Philippi, 1853) is known from Queensland, New South Wales and southern Australia, though absent from Tasmania (Wilson & Gillett 1971) and Western Australia (Wells & Bryce 1985). *Polinices incei* was reported by Wilson & Gillett (1971) and Ludbrook & Gowlett-Holmes (1989) to live in the mid-littoral zone of high-energy surf beaches although, curiously, Wilson

(1993: 220; 2002: 120) reported it as living on 'muddy substrates' and 'muddy flats', respectively, a habitat more typical of *Polinices sordidus* (Swainson, 1821) and *P. melanostomus* (Gmelin, 1791), at least in the Moreton Bay region. The present study confirms that *P. incei* really is a specialised inhabitant of wave-exposed beaches, and thus a highly unusual naticid. *Polinices incei* has been surprisingly little studied, except for an examination of its burying and crawling behaviour in response to diesel oil contamination (Chapman *et al.* 1988), and a report that it responds positively to sound (Kitching & Pearson 1981). The former authors showed that diesel oil produced a significant response in terms of burial and crawling activity, whereas the latter authors speculated that the response of *P. incei* to sound may assist in capturing prey. Surprisingly, however, no one has commented upon the uniqueness of such a high energy habitat for a naticid and, consequently, the different behaviours that *P. incei* must have developed for such an unusual mode of life. This forms the subject of the present paper.

MATERIALS AND METHODS

From 9–22 February 2005 a number of exposed surf beaches on North Stradbroke Island were regularly visited on falling tides. These included Frenchman's Bay, Main Beach, Home Beach, Cylinder Beach and Blue Lake Beach. It became apparent, that *Polinices incei* was most abundant on the most exposed Blue Lake Beach, and its resident population thus became the object of more detailed study. Captured individuals of *P. incei* from the other beaches were also kept and used in laboratory experiments to examine behaviour in more detail.

In addition, field observations of *Polinices incei* from One Mile Beach, Port Stephens, New South Wales, were also made.

FIELD STUDIES

Habitat sediment analyses. At each 10 m interval down shore from the approximate position of mean high water tide at Blue Lake Beach, samples of sand were taken and sediment analysis undertaken using a series of graded sieves (16,000, 8,000, 4,000, 2,000 and 1,000 μm). Sediment particle size distributions < 1,000 μm were determined using a Malvern

Mastersizer 2000 particle sizer. Such data have previously been validated by comparison with wet sieving (Hart 1996) and such Mastersizer output describes particle size distributions in terms of mean phi (f), fraction percentages (coarse sediments, sands and fines), sorting (mixture of sediment sizes) and skewness (weighting of sediment fractions > and < the mean sediment size) (Folk & Ward 1957). Also analysed were total organic contents of the sediment samples calculated as percentage losses on ignition (LOI).

Parameters which had different values among samples, including mean mm, mean f, and total organic content (% LOI), were subjected to non-parametric multivariate analysis using PRIMER Version 5 (Clark & Gorley 2001), to identify differences in them among shore levels. A similarity matrix was constructed using the Bray-Curtis similarity measure, and multidimensional scaling (MDS) was performed to visualise the parameters which varied among samples, that is, mean mm, mean f and organic content.

Distributions and population structures of *Donax deltoides* and *Polinices incei*. At each 10 m interval down the shore of Blue Lake Beach, the occurrence of dominant macrofaunal species were identified. In addition, 1 m x 1 m quadrats were laid out from the approximate position of mean high water mark and scraped to a depth of 5 cm to determine numbers of infauna, that is, largely, the bivalves *Donax deltoides* Lamarck, 1818, and *Polinices incei*.

Empty *Donax deltoides* shells and *Polinices incei* individuals. For five days, the sands of Blue Lake Beach were searched for living individuals of *Donax deltoides* and *Polinices incei* (in particular, the trails of foraging individuals) and the empty shells of *D. deltoides*. Each living and empty shell (or single valves) of *D. deltoides* was measured along its greatest length to the nearest 1 mm, and the latter examined for the presence of drill holes. In the case of *P. incei*, each captured individual was measured in the field along its greatest shell width to the nearest 0.1 mm using vernier calipers. It was then examined to see if it was feeding or holding prey items in its foot. If so, the numbers and shell lengths of the captured *D. deltoides* individuals were recorded and the positions of any drill

holes (and attempts) recorded on a master diagram of the species.

These observations on *Donax deltoides* and *Polinices incei* individuals were repeated over a lesser period of three days at One Mile Beach, Port Stephens, New South Wales.

BEHAVIOURAL STUDIES (FIELD AND LABORATORY)

Blue Lake Beach and One Mile Beach were watched to determine aspects of the behaviour of *Polinices incei*. This also resulted in some aspects of the behaviour of *Donax deltoides* being recorded.

In the laboratory, *Polinices incei* individuals collected from Frenchman's Bay, Main Beach, Home Beach and Cylinder Beach were kept in trays of aerated seawater changed daily. Aspects of the locomotion of *P. incei* were examined using lines drawn 10 mm apart on the bottom of the trays and a stopwatch. When the water in the trays was agitated, *P. incei* individuals turned on their backs, as will be described. Ten *Polinices incei* individuals were also kept for a period of 10 days in trays with 20 small (<10 mm shell length) individuals of *Donax deltoides*, but none were attacked and this trial is not reported upon further.

As will be described, five *Polinices incei* individuals were found drilling *Donax deltoides* in the field. The drilled shells were cleaned in an ultrasonic shaker, sputter coated with gold, and examined using scanning electron microscopy (Jeol 820) at the University of Cambridge, England.

RESULTS

FIELD STUDIES

Habitat sediment analyses. Results of the downshore sediment analysis (0–80) at Blue Lake Beach are given in Table 1. Mean particle size ranged from 282–397 μm with the highest values > ~300 μm being recorded from the lower half of the shore. All sediments were, however, classified as well sorted (φ units ranging from >1.70 to < 170 at the upper and lower levels of the beach, respectively), medium sand with a very low total organic content (< 0.3% Loss on Ignition). Statistical analysis of the dataset identified differences in sediment composition down the shore at Blue Lake Beach and MDS results (Fig. 1) show that sand from shore levels 0–10 m, 10–20 m, 20–30
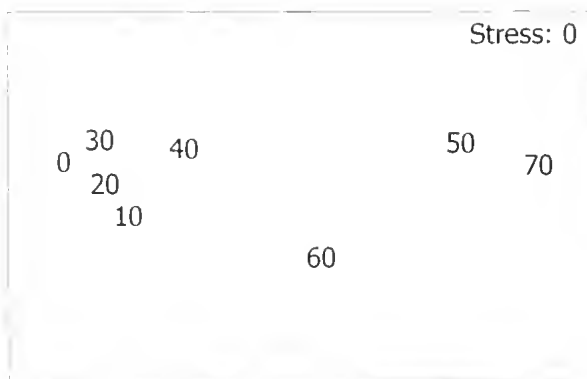

FIG. 1. Multivariate analysis of the particle size dataset for the sands of Blue Lake Beach, North Stradbroke I., Queensland, using the Bray-Curtis similarity matrix and non-metric multidimensional scaling (MDS) ordination in two dimensions.

m, 30–40 m and 40–50 m were similar, and different from shore levels 50–60 m, 60–70 m and 70–80 m. That is, mean particle size and φ at the former levels were all <300 μm and >1.75 respectively, whereas the latter were all >300 μm and <1.75 respectively.

Population structure of *Donax deltoides*. Table 2 shows the ranges and means of living shells and drilled valves (by an unknown predator) of *Donax deltoides* on Blue Lake Beach (plus Main Beach for comparison), and One Mile Beach, NSW. Mean shell lengths for undrilled and drilled shells for Blue Lake Beach and One Mile Beach were 44.2 mm and 31.2 mm (43.6 mm and 34.2 mm for Main Beach) and 38.3 mm and 28.4 mm, respectively. Generally, therefore, *D. deltoides* individuals (both undrilled and drilled) from One Mile Beach were smaller than conspecifics from North Stradbroke Island.

Length frequency histograms of the population of *Donax deltoides* on Blue Lake Beach are illustrated in Fig. 2. This composite figure shows that living individuals collected during all surveys ranged in shell length from a minimum of 3.2 mm to a maximum of 56.9 mm. There appear to be peaks at shell lengths of 0–10 mm, 35–40 mm and 50–55 mm. These may represent age cohorts, but in the absence of data from other months this cannot be confirmed. However, it is clear that <10 mm individuals are juveniles.

The incidence of drilling predation by *Polinices incei* on *Donax deltoides*. Table 3
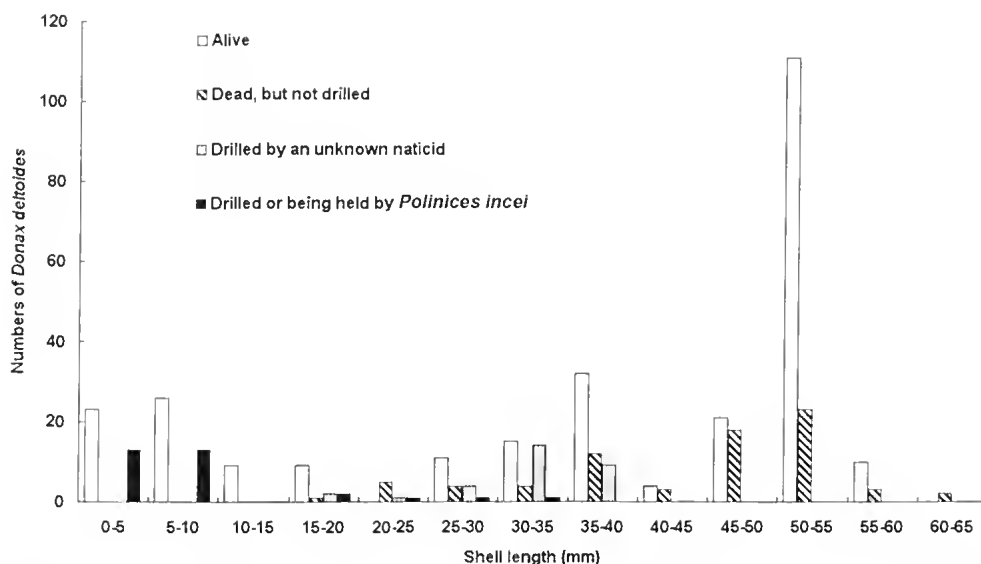
FIG. 2. *Donax deltoides*. The shell length frequencies of living individuals, empty (undrilled) shells, valves drilled by an unknown naticid and individuals observed to be either being drilled or held *by Polinices incei* on Blue Lake Beach, North Stradbroke Island, Queensland.

shows the size distribution of *Donax deltoides* individuals from Blue Lake Beach and One Mile Beach that were known to be either drilled or being held by *Polinices incei*. The bivalves ranged in shell length from 3.1–29.5 mm (mean = 7.6) with a peak in 0–10 mm individuals in the case of Blue Lake Beach, and 2.2–18.7 mm (mean = 5.0) with a peak also in 0–10 mm individuals in the case of One Mile Beach. Results of a

t-test show that the populations of *D. deltoides* on Blue Lake Beach and One Mile Beach were not significantly different in terms of shell size ($p < 0.02$).

Table 3 also shows the size distribution of *Polinices incei* individuals from Blue Lake Beach and One Mile Beach. The species had mean shell lengths of 12.2 mm on Blue Lake Beach and 9.5 mm on One Mile Beach. That is, the mean size

Table 1. Particle size analysis of the sands of Blue Lake Beach, North Stradbroke Island, Queensland and the approximate pattern of zonation of characterising macrofaunal species and estimates of the numbers of *Donax deltoides* and *Polinices incei* • m². Otherwise, all samples comprised well-sorted medium sand with 0% fine (<63 ìm) and coarse (>2 mm) sand and 100% medium sand.

Metres down shore from MHTL	Mean particle size (µm)	Mean phi	Total organic content (% LOI)	Characterising species	Numbers D. deltoides/ P. incei per m²
0 – 10	289	1.79	0.3	Adult *Ocypode ceratophthalma*	
10 – 20	294	1.77	0.2	Juvenile *Ocypode ceratophthalma* + *Scopimera inflata*	
20 – 30	289	1.79	0.2		
30 – 40	282	1.82	0.2	Adult *Donax deltoides*	96
40 – 50	298	1.75	0.1	Adult + juvenile *D. deltoides*	96 + 48/**16**
	368	1.44	0.1	Juvenile *D. deltoides*	0 + 16/**32**
60 – 70	337	1.57	0.2	Juvenile *D. deltoides*	0 + 16/**16**
70 – 80	397	1.33	0.1	Occasional *D. deltoides*	

Table 2. Ranges and means of shell lengths of undrilled and drilled *Donax deltoides* individuals on Blue Lake Beach, North Stradbroke Island and One Mile Beach, Port Stephens. *Data for drilled and undrilled shells collected from Main Beach, North Stradbroke Island, are also given for comparison with Blue Lake Beach.

Beach	Mean shell length undrilled (mm)	Range shell length undrilled (mm)	Mean shell length drilled (mm)	Range shell length drilled (mm)
Blue Lake Beach	44.2	17.3 – 60.7	31.2	15.0 – 38.2
*Main Beach	43.6	21.3 – 62.8	34.2	31.4 – 38.6
One Mile Beach	38.3	15.3 – 61.2	28.4	14.6 – 35.2

Table 3. Results of a *t*-test to determine differences in the shell width (mm) of *Polinices incei* and the shell lengths (mm) of *Donax deltoides* individuals being either drilled or held between A, Blue Lake Beach, North Stradbroke Island, Queensland, and B, One Mile Beach, Port Stephens, New South Wales. The null hypothesis is rejected when $p < 0.05$.

Taxon	Site	*t*-test, p	*t*-test, df	N	Mean ± S.E. (mm)	Range (mm)
Polinices incei	A	0.002	66	34	12.19 ± 0.74	1.6–22.3
	B			34	9.53 ± 0.39	5.9–15.5
Donax deltoides	A	0.02	73	38	7.61 ± 0.99	3.1–29.5
	B			37	5.01 ± 0.42	2.2–18.7

of *P. incei* was significantly larger (p=0.002) on Blue Lake Beach, possibly explaining why larger *Donax deltoides* prey were attacked on the former beach (see above).

The sizes of empty undrilled shells of *Donax deltoides* (intact and right valves only) on Blue Lake Beach (Fig. 2) ranged from 10.7–62.8 mm, with peaks again of 35–40 mm and 50–55 mm shell lengths matching those values, save for the juveniles, identified for the resident living *Donax deltoides* population (also Fig. 2). The shell lengths of drilled (by an unknown naticid predator) *D. deltoides* collected from Blue Lake Beach ranged from 15.0–38.6 mm with a peak in the 30–35 mm size class (Fig. 2). The shell lengths of *D. deltoides* individuals from One Mile Beach observed to be either being held or drilled by the predator *Polinices incei* ranged from the 0–5 mm to 30–35 mm size classes (Fig. 2). That is, there is considerable overlap between the *D. deltoides* shells drilled by an unknown naticid and those individuals observed being attacked by *P. incei*.

Population structure of *Polinices incei*. The population structures of *Polinices incei* individ-uals inhabiting Blue Lake Beach and One Mile Beach are illustrated in Fig. 3. At both localities there is a peak of individuals ~10 mm in shell width. A greater range in shell widths was obtained from Blue Lake Beach, that is, from 16–22.3 mm, whereas on One Mile Beach the range was from 5.9–15.5 mm (Table 3). It seems clear therefore that in both locations, the intertidal components of the two populations mainly comprise juvenile individuals. On the basis of growth rings present in its statoliths, Richardson *et al.* (2005) showed that *Polinices pulchellus* (Risso, 1826) lives for a maximum of two to three years.

MORPHOLOGY AND BEHAVIOUR OF *POLINICES INCEI*

Morphological characteristics. The shells of *P. incei* are rounded with a very depressed, low spire. Size ranges up to 19 mm in height and 28 mm in width (Ludbrook & Gowlett-Holmes 1989). Individuals collected in this study ranged in shell width from 5.7–29.3 mm. A button-like callus within the umbilicus, surrounded by a groove, characterises the ventral surface of the shell. The most distinguishing feature of the shell dorsally, however, is its colour polymor-phism (Fig. 4). Colours range from cream, pale
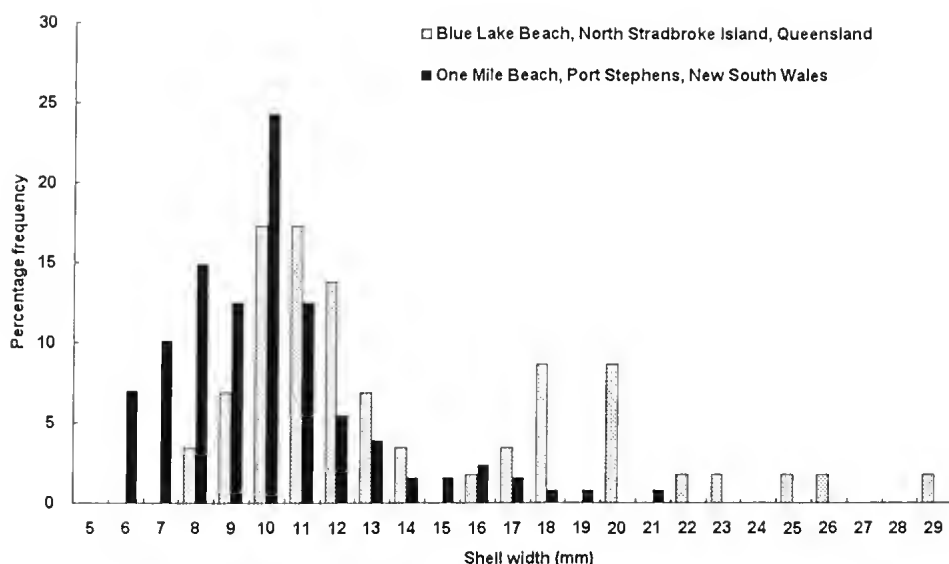
FIG. 3. The size (shell length) frequencies of the populations of *Polinices incei* on Blue Lake Beach, North Stradbroke Island, Queensland, and One Mile Beach, Port Stephens, New South Wales.

yellow, grey, brown, purple and near black, although the spire is often patterned variably. Figure 5 illustrates shells representing the full spectrum of colours. There seems to be a progressive loss of the purple/black coloration towards cream, but then an increase, or replacement, with brown. Clearly the blacks morphs stand out most clearly on the clean beaches of eastern Australia, whereas the other colour morphs are more cryptic in such sands that contain fragments of shells, stones and other marine debris.

The unusually dorso-ventrally flattened form of *Polinices incei* is best illustrated by comparison with *Polinices sordidus* (Swainson, 1821)
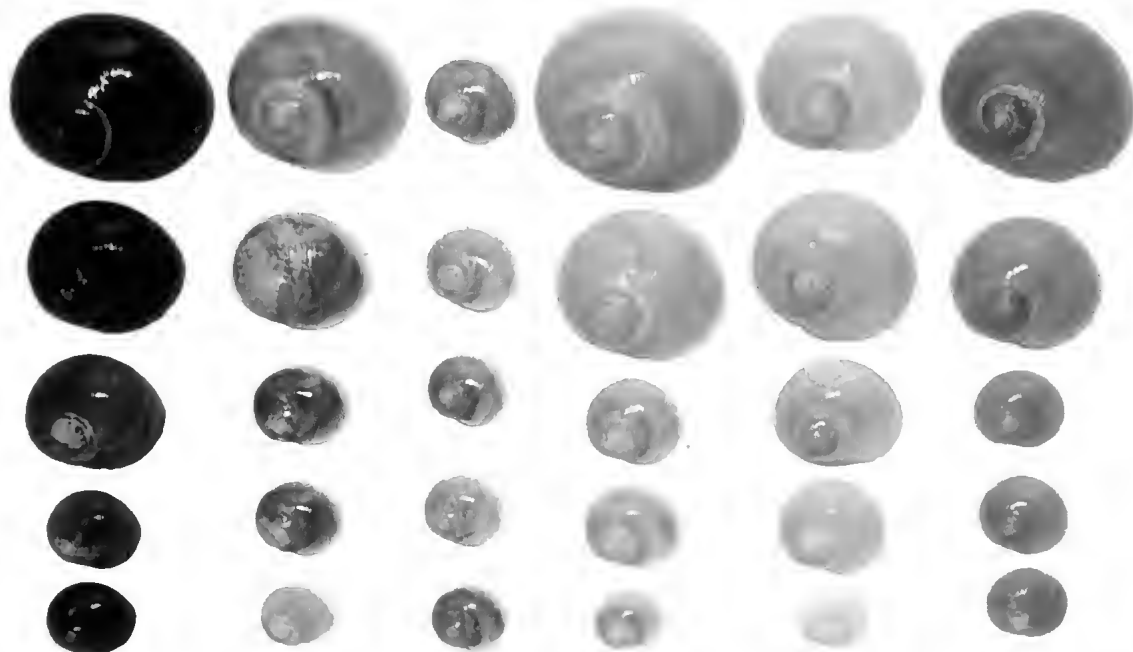

FIG. 4. *Polinices incei*. The range of colour polymorphism expressed on the dorsal surface of the shell.
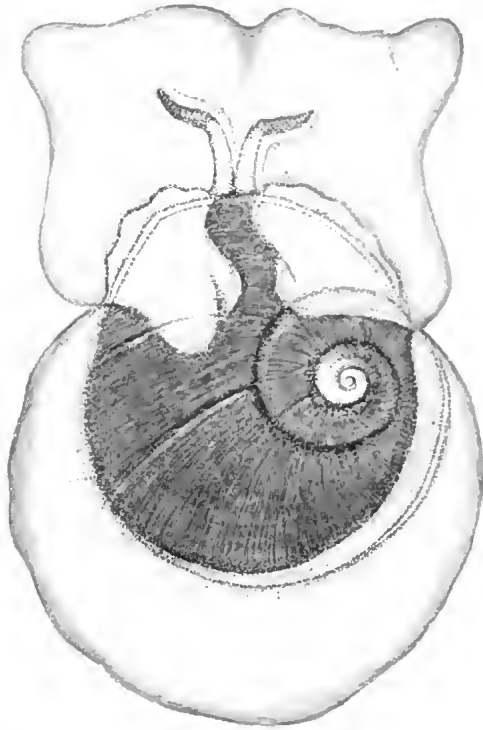
FIG. 5. *Polinices incei*. A black-shelled individual as seen from the dorsal aspect.
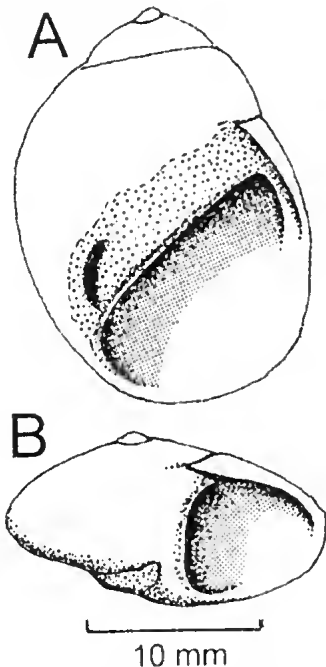

10 mm

FIG. 6. Ventral views of **A**, *Polinices sordidus*, and **B**, *Polinices incei*, both drawn to the same scale.

from the sheltered, muddy shores of Moreton Bay on the west side of North Stradbroke Island (Fig. 6). The latter species (Fig. 6A) is conically ovate, with a moderately high spire, and has a maximum shell height and width of 49 mm and 45 mm, respectively. That is, a height to width ration of ~ 1:0.98. In comparison, the height to width ration of *P. incei* is ~1:1.37 (Fig. 6B).

Behaviour of *Donax deltoides*. On both Blue Lake Beach and One Mile Beach, *Donax deltoides* is tidally migratory. Most obviously, large individuals emerge from the sand and are tumbled down the beach in the backwash during periods of falling tides. Smaller individuals were rarely observed doing this, but this might simply be a reflection of the observer's inability to see them migrating. Notwithstanding, *Polinices incei* does migrate up the shore during rising tides and remains there to hunt resident small *D. deltoides* individuals.

Behaviour of *Polinices incei*. As the tide recedes on the exposed beaches of North Stradbroke Island and One Mile Beach, individuals of *P. incei* are exposed. Densities are, however, low (<1 individual 10 m²). Typically, individuals are solitary, burrow to a shallow depth (Fig. 7A) and leave meandering trails at the sand surface as the tide falls. Such trails are obliterated by the swashes of the periodically larger waves, but in intervals between such surges, the trails can lead to the capture of the individuals making them. This is especially true towards the top of the beach, but lower down the regular swash obliterates the trails making individuals harder to find. Several behaviours of *P. incei* were identified. These included:

Surfing. An unusual behaviour is here termed surfing. In aquarium trays, most *P. incei* moved across the bottom, however when small imitation waves were created by lifting the trays up and down at one end, individuals turned onto their backs, and the foot and propodium became hugely inflated (Fig. 7B & C) such that the animals became buoyant and were washed to and fro. This behaviour is interpreted as a way for *P. incei* to quickly reach higher levels of the shore to hunt for small *Donax deltoides*. Clearly, to crawl up a beach that may be over one hundred metres wide, over each tidal cycle, would be impossible.

Surfing by *P. incei* was observed in the field only on a falling tide and in the backwash, at
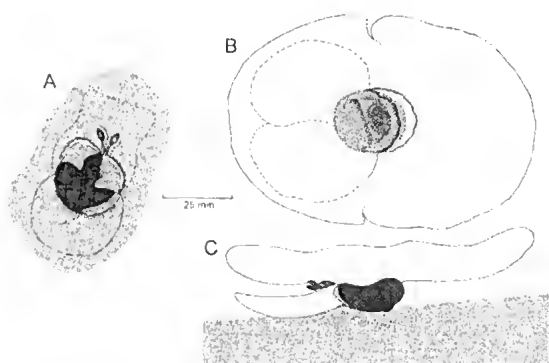
FIG. 7. *Polinices incei.* **A**, dorsal view of a burrowing individual; **B**, **C**, ventral and lateral views of an inflated, surfing individual (all drawn to the same scale).
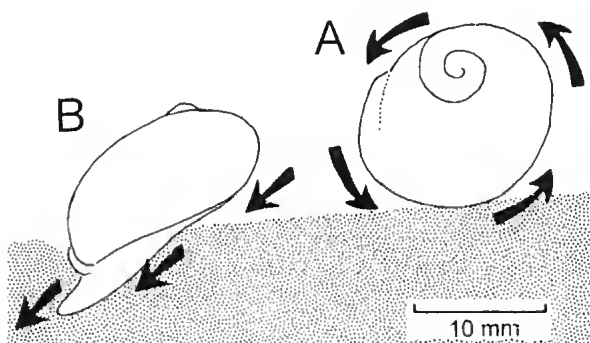
FIG. 8. *Polinices incei.* Illustrations of **A**, a retracted individual rolling down the beach, and **B**, a braking individual with only slightly extended propodium and foot.

both Blue Lake Beach and One Mile Beach. It was impossible to observe on the rising tide as the breaking waves put too much sand into suspension for clear observations. This inability to observe migrating or surfing animals at this critical time has also been commented upon by Odendaal *et al.* (1992). Notwithstanding, as the tide and wave backwashes recede, *P. incei* individuals are observable emerging instantaneously from the sand and inflating the foot and propodium so as to be rapidly carried downshore. Many such individuals were determined also to be carrying prey in the foot (Table 4).

Braking. One aspect of the behaviour of *P. incei* often observed on Blue Lake Beach and One Mile Beach was braking. When individuals higher on the shore were exhumed from the sand by a breaking wave, or were attempting to
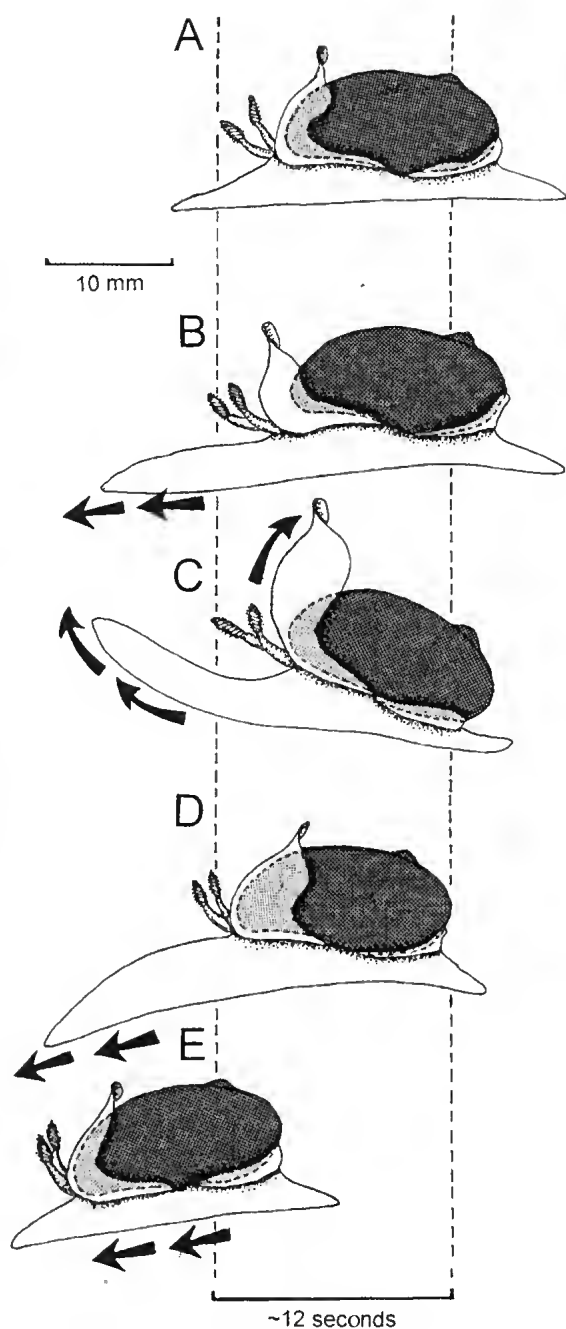
FIG. 9. *Polinices incei.* **A–E**, Stages in the sequence of galloping locomotion.

relocate downshore (sometimes with captive prey held by the foot), they retracted the body into the shell and rolled down the beach in the backwash (Fig 8A). At some point, however, the anterior region of the foot and the propod-

Table 4. The numbers of cases of drilling predation, prey holding (1, 2 or 3 prey items) and prey chasing by *Polinices incei* on *Donax deltoides* on A, Blue Lake Beach, North Stradbroke Island, Queensland, and B, One Mile Beach, Port Stephens, New South Wales. (* indicates *P. incei* individuals actively surfing down shore with captured prey individuals).

Site	Predator/prey interaction	Number of cases	Mean shell width/ **length** of predator/**prey** (mm)
Blue Lake Beach	Drilling	4	18.2 / **23.4**
	Prey holding	22 (19 x 1; 2 x 2; 1 x 3 prey items)	11.3 / **5.9**
	Prey nearby	9	12.4 / **5.3**
	Prey chasing/ escaping	1 (11.3 / **5.0**)	
One Mile Beach	Drilling	1	15.5 / **22.4**
	Prey holding	27 (22 x 1*; 5 x 2 prey items**)	9.3 / **4.6**
	Prey nearby	4	8.4 / **4.6**
	Prey chasing/ escaping	None observed	

Table 5. Predator shell width, prey shell length and outer borehole diameter data for the five examples of *Polinices incei* attacking *Donax deltoides* on Blue Lake Beach, North Stradbroke Island, Queensland, and *One Mile Beach, Port Stephens, New South Wales.

	Polinices incei shell width (mm)	*Donax deltoides* shell length (mm)	Valve drilled / attempt	Outer drill hole / attempt diameter (mm)
	22.3	29.5 + attempt	Left / Left	1.5 / 1.1
	20.3	25.6 + attempt	Left / Left	1.3 / 1.1
	19.8	23.1	Right	1.2
	10.5	15.2	Left	0.6
	15.5*	18.7*	Left*	1.1*
Mean	**17.7**	**22.4**	**4 Left x 1 right**	**1.1 / 1.1**

ium was extended a short distance causing, on succeeding rolls, the animal to halt its down-shore progress and end up in a position enabling it to instantly resume locomotion (Fig. 8B).

Hunting. P. incei hunts within the sand, typically at depths of 5–10 mm such that no part of the shell or body is visible at the surface. Only a meandering surface trail marks the progress of an individual. In laboratory aquarium trays, measured normal locomotory speeds of *P. incei* ranged from 9–17 seconds · cm^{-1} (n=20), with a mean of 12 seconds · cm^{-1}.

Galloping. On the surface of the sand, it was occasionally observed that *P. incei* engages in a second form of locomotion to the usual slow crawling. This may be related to more active prey pursuit. The speedier locomotion is termed galloping and is illustrated in Fig. 9. When seen from the side, the posterior part of the foot that is normally extended posteriorly (A), is sharply retracted (B). The cephalic lobes and anterior region of the foot are then extended upwards, the latter being extended dramatically (C). The greatly anteriorly elongate foot is then extended forwards where it grips the sand (D). It then contracts rapidly pulling the body forwards (E), such that the original position in (A) is obtained but ~ half a shell length further forward. Speeds obtained during galloping (in aquarium trays) ranged from 5–11 seconds · cm (n = 20), with a mean of 8 seconds · cm.

Prey holding. Polinices incei actively forages on the surf beaches of North Stradbroke Island, most notably Blue Lake Beach, and on One Mile
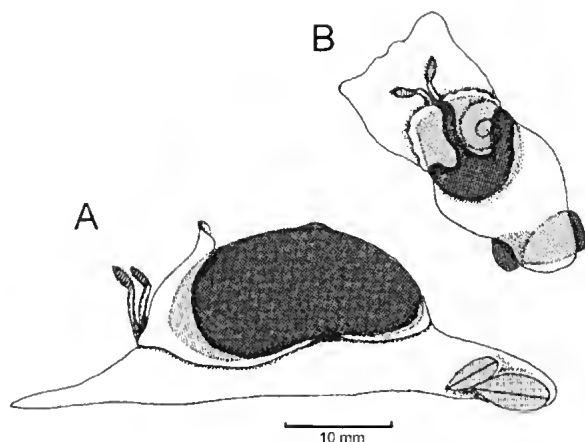
FIG. 10. *Polinices incei*. **A**, dorsal, and **B**, lateral views of an individual holding a captured prey item of *Donax deltoides* under the posterior end of the foot.

Beach, NSW. Table 4 identifies the numbers of cases of a) prey drilling; b) prey holding (including the numbers of cases of 1, 2 or 3 prey items being held); c) incidences of prey and predator near to each on the sand surface; and d) incidence of a prey actively trying to escape a pursuing predator, on both beaches. In all cases, the captured *Donax deltoides* individuals were held in place by mucus under the posterior edge of the foot, as illustrated in Fig. 10. Altogether, 22 individuals of *P. incei* (mean shell width = 11.3 mm) were identified holding their prey (mean shell length = 5.9 mm) in such a manner on Blue Lake Beach. Of these, 19 were holding 1, two were holding two, and one was holding three prey items. On One Mile Beach, 27 cases of prey holding by *P. incei* (mean shell width = 9.3 mm) were identified. Of these 22 were holding one, and five were holding two prey items. Mean shell length of the *D. deltoides* prey was 4.6 mm. On Blue Lake Beach and One Mile Beach there were nine and four cases of predator (mean shell widths of 12.4 mm and 8.4 mm, respectively) and prey (mean shell lengths of 5.3 mm and 4.6 mm, respectively) items close together on the sand surface, respectively, whereas on the former beach one case of a *D. deltoides* (shell length = 5.0) prey actively trying to escape a *P. incei* individual (shell width = 11.3 mm) was observed (Fig. 11). In addition, on One Mile Beach (Table 5*), there were three observed cases of *P. incei* surfing downshore each holding either one (x 1) or two (x 2) *D. deltoides* prey items.
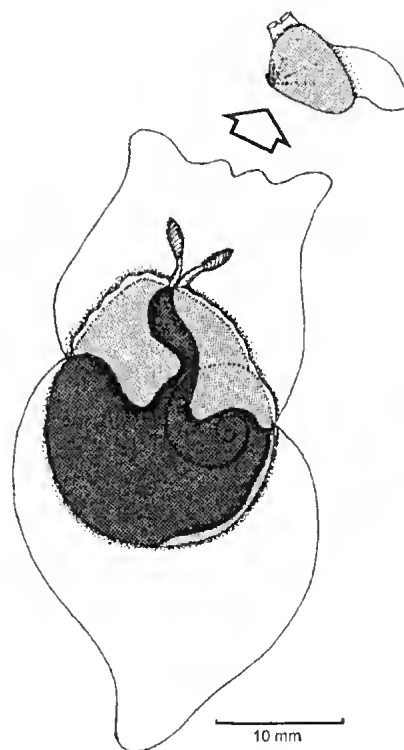
FIG. 11. *Polinices incei*. An individual high on the shore chasing a juvenile *Donax deltoides* that is attempting to escape by leaping.

The relationships between predator *Polinices incei* shell width and either drilled or captured prey (*Donax deltoides*) shell length for Blue Lake Beach and One Mile Beach are illustrated in Fig. 12 (● and ○, respectively). The slopes of the data plots are generally similar. Generally too, the shell lengths and widths of the *D. deltoides* and *P. incei* populations (in both cases including actual prey and predator sizes) on One Mile Beach, New South Wales are smaller than their conspecifics on Blue Lake Beach, Queensland (Tables 2, 3 & 4).

Prey consumption. Four cases of *Polinices incei* successfully attacking *Donax deltoides* were identified on Blue Lake Beach and one on One Mile Beach (Tables 4 & 5). In these cases, the attack was as described for other naticids with the bivalve being held by the foot, and with the proboscis, mostly obscured by the propodium, involved in drilling the prey shell. Four attacks (plus two initial attempts) were on the left valve and one on the right. There is not only a positive

FIG. 12. The relationships between predator (*Polinices incei*) shell width and prey (*Donax deltoides*) shell length of individuals collected from (●) Blue Lake Beach, North Stradbroke Island, Queensland and (o) One Mile Beach, Port Stephens, New South Wales.

relationship between predator shell width and prey shell length but also a relationship between predator shell width and drill hole diameter, larger individuals making larger drill holes (Table 5).

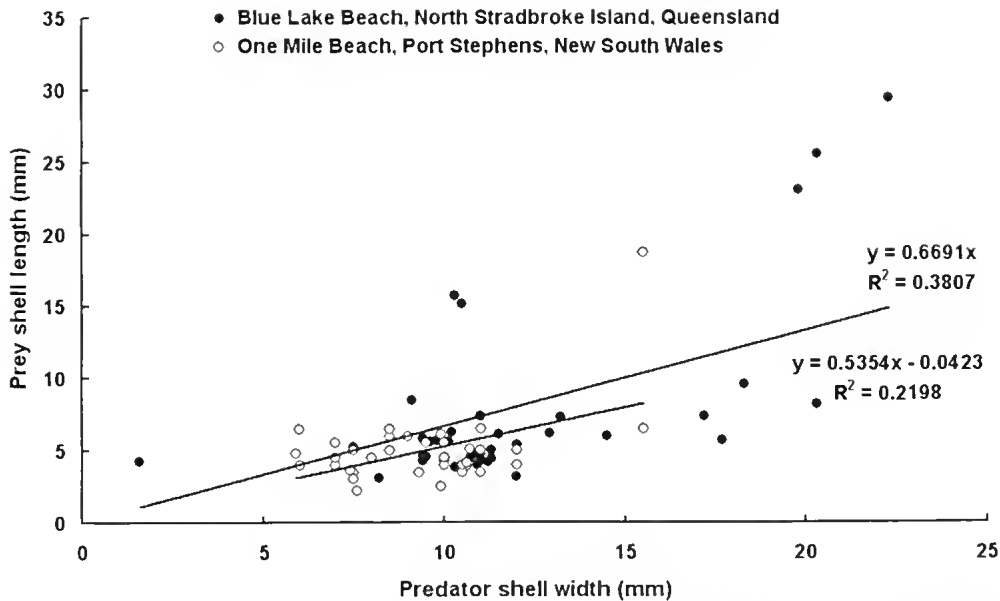The positions of the five identified drill holes made in the shells of its *Donax deltoides* prey by *Polinices incei* are illustrated in Fig. 13. Four attacks were identified from Blue Lake Beach,
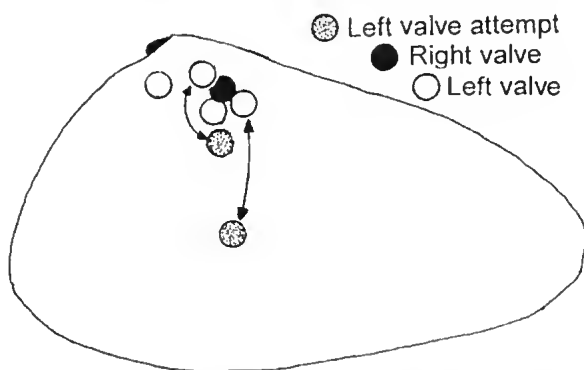
FIG. 13. The positions of drill holes made in the shells of five individuals (plus two abandoned attempts) of *Donax deltoides* by *Polinices incei* from Blue Lake Beach, North Stradbroke Island, Queensland, and One Mile Beach, Port Stephens, New South Wales.

three on the left valves and one on the right, plus two abandoned attempts on left valves below two of the above identified attacks. Only one attack on the left valve was identified for One Mile Beach. All attacks were close to the umbones of *D. deltoides*, that is, at a position above the digestive diverticula. The two initial attempts were more ventral to the final adopted attack site, suggesting that the predator chose to finalise its attack more dorsally.

Four drill holes and the one abandoned attempt are illustrated as SEM photomicrographs in Figs 14 and 15. Figure 14A shows the abandoned attempt wherein only the periostracum has been removed but interestingly by etching not radula scraping. In Fig. 14B, the drill hole is deeper showing evidence again of chemical etching. Fig. 14C shows how a central 'boss' has been created in the centre of the drill hole, while Fig. 14D illustrates a completed, countersunk drill hole characteristic of naticids (Ziegelmeier 1954; Carriker 1981). Fig. 15 shows another early drill hole (~ equivalent to Fig. 15B) with a near circular countersunk hole and Fig. 15B is a higher magnification of the periostracum around this hole showing clear evidence of chemical etching.

FIG. 14. *Donax deltoides*. Scanning electron micrographs (Jeol 820) of four drill holes made by *Polinices incei*. **A**, An abandoned attempt showing that the periostracum has been removed by etching; **B**, drilling has commenced creating a characteristic near circular, countersunk drill hole; **C**, drilling nearly complete with a characteristic central boss to the drill hole; and **D**, a completed drill hole.
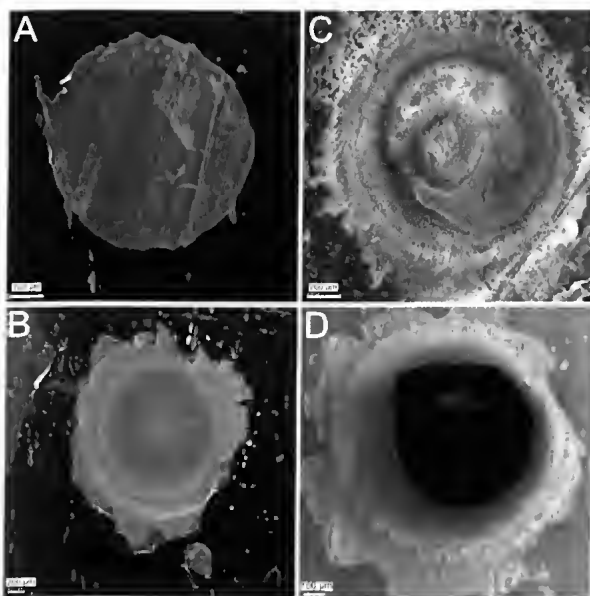

FIG. 15. *Donax deltoides*. Scanning electron micrographs (Jeol 820) of **A**, an initially etched shell and periostracum approximately equivalent to Fig. 14B, and **B**, a higher magnification micrograph of the chemically etched periostracum and dissolved shell material.

DISCUSSION

The earliest holes resembling those of naticids are Triassic between ~195–225 mya (Newton 1983; Fursich & Jablonski 1984), although the group diversified, alongside the Muricidae, in the Cretaceous between 65–136 mya (Sohl 1969; Kabat 1990). Today, this diverse group of predators is dominant on soft substrata virtually worldwide, while representatives of the Muricidae are more common on hard substrata. Both, however, largely but not exclusively, drill their prey. Ziegelmeier (1954), Carriker (1981), Kitchell (1986), Kabat (1990) and Reyment (1999) have reviewed naticid predation.

Temperate shore predators such as the muricids *Nucella lapillus* (Linnaeus, 1758) and *Urosalpinx cinerea* (Say, 1822) attack shells both mechanically by rasping with the radula, and chemically using the secretion of the accessory-boring organ (ABO) (Gabriel 1981). *Urosalpinx cinerea* largely uses its radula to scrape holes in the shells of *Mytilus edulis* Linnaeus, 1758, and

Mya arenaria Linnaeus, 1758 (Carriker *et al.* 1974). Radula scrape marks were also identified from the holes drilled by *Lepsiella paivae* (Crosse, 1864) in its bivalve prey, the venerid *Katelysia scalarina* (Lamarck, 1818) (Morton 2005). Notwithstanding, the accessory boring organ is considered to be an essential component of the shell penetrating mechanism of drilling gastropods (Carriker 1981). It is located in the foot of Muricidae and is responsible for producing acidic secretions, chelating agents and enzymes (Carriker & Williams 1978; Carriker 1981). Carriker & Williams (1978) hypothesised that drilling by muricid gastropods employs a combination of enzymes, an inorganic acid, chelating agents in a hypertonic medium to facilitate shell dissolution, and intracellular transport of calcium during the chemical phase of valve penetration.

Ponder & Taylor (1992, plates III & IV) provided SEM pictures of the drill holes made by *Austroginella johnstoni* in various bivalve prey while Ansell (2000: fig 2A–D) illustrates the structure of drill holes made by the New Zealand *Xymene plebeius*. Harper & Peck (2003, fig. 2A–D) illustrate the holes made by *Trophon longstaffi* in its bivalve prey, the Antarctic laternulid *Laternula elliptica*, and those made by *Lepsiella paivae* in the shells of *Katelysia scalarina* were illustrated by Morton (2005: figs 3, 4).

Ponder & Taylor (1992) could not identify radula scrape marks in the excavations made on the shells of bivalve prey by the marginellid *Austroginella muscaria* (Lamarck, 1822). Both the crossed-lamellar and homogeneous shell micro-

structures exposed in the excavations were all highly corroded with the aragonite crystals having rounded edges. This suggested a dominantly solutional, rather than mechanical, drilling mechanism. Similarly, an SEM study of the holes drilled by *Hexaplex trunculus* (Linnaeus, 1758) (Muricidae) in the shells of various species of bivalve prey by Peharda & Morton (2006) found no evidence of radula scrape marks. The scanning electron microscope images revealed etched shell surfaces indicating chemical shell penetration.

Unlike the mainly chemical method of prey shell access in representatives of the Muricidae and Marginellidae, however, drilling in the Naticidae is thought to involve mechanical radula rasping and secretions from an accessory boring organ (ABO) located in the proboscis (not the foot as in muricids). The secretions produced by the naticid ABO comprise hydrochloric acid, enzymes and chelating agents (Carriker & Gruber 1999). Prey is first detected by chemo- and/or mechano-reception, evaluated by handling and, if accepted, engulfed in a gelatinous mucous and finally enveloped and oriented by the propodium in preparation for drilling. Unlike straight-sided muricid drill holes, those made by naticids are beveled and parabolic in cross section such that the outer drill hole diameter is larger than the inner (Bromley 1981; Carriker 1981; Kowalewski 1993; Reyment 1999). Zeigelmeier (1954) described the drilling mechanism in *Lunatia nitida* (Donovan, 1800) — during prey shell penetration, the proboscis is rotated by 90° at a time and radula rasping is undertaken systematically, sector by sector, from the centre of the developing drill hole to the periphery. The centre of the hole where the least radular rasping occurs is thereby formed into a boss that is characteristic of naticid drill holes. Such a boss is also seen in the holes drilled by *Polinices incei* (Fig. 14C). According to Zeigelmeier (1954), radula rasping is followed by raising the proboscis from the incomplete drill hole and placing the ventral lip of the mouth containing the ABO in the hole. Secretions from the ABO dissolve the shell layers, and the weakened shell is further radula rasped to complete the drill hole. Zeigelmeier (1954) also noted that *L. nitida* swallowed the

shell material produced in the process of drilling. However, in the *Donax deltoides* shells herein examined using the SEM, there is no indication of radula rasping (Figs 14 & 15) at any stage of the shell penetration process.

Aquarium observations of naticid gastropods in Hong Kong showed that different species attack their bivalve prey in different ways (Ansell & Morton 1987). *Polinices tumidus* has been shown to adopt at least three different tactics in dealing with bivalve prey, that is, conventional side drilling, edge drilling, and non-drilling predation. None of these is used exclusively against any particular prey, at least not under aquarium conditions, but the frequency of occurrence of a particular method differs with different prey. No clear relationship between prey shell thickness and degree of shell ornamentation and the percentage of non-drilling attacks was identified (Ansell & Morton 1987).

Taylor *et al.* (1969) examined the shell microstructure and mineralogy of four species of *Donax*. In all cases, the aragonitic shell comprised three layers, that is, an outer composite prismatic, a middle crossed lamellar and inner complex crossed lamellar layers. The prismatic outer layer is believed to give the best protection against drilling gastropods, and possibly other shell-penetrators (Gabriel 1981). Although protection from shell drilling predators may have been a major factor in the evolution of shell types, it is clear that *Polinices incei* has overcome the inherent resistance to abrasion by the outer prismatic layer of the *Donax deltoides* shell and penetrates it chemically. Harper & Skelton (1993a) suggest that the inert bivalve periostracum confers a degree of protection against drilling predators by retarding penetration of the ABO secretion. The same authors (Harper & Skelton 1993b) demonstrated this for mytilid bivalves that with the periostracum stripped from the shells were more vulnerable to muricid drilling predation than those with the periostracum intact.

This is clearly not the case, however, for *P. incei* attacking *D. deltoides* using ABO secretions, and thus raises the question whether the periostracum does have any role in protecting the bivalve shell from penetration by either mechanical or chemical erosion.

Many predatory gastropods detect their prey by chemoreception (Kohn 1961). Nassariid gastropods, like naticids, do not generally occupy high energy, wave-exposed, beaches, chemical cues emanating from stranded carrion being better detected on long, gently sloping beaches under conditions of low exposure to wave action (Britton & Morton 1994). A remarkable exception to this generalisation is *Bullia digitalis* in South Africa that 'surfs' or swash-rides up wave-exposed shores in search of carrion, for example, stranded jellyfish (Odendaal *et al.* 1992). *Polinices incei* lacks eyes, as in other swash riders such as species of *Bullia*. Instead the latter has an acute sense of smell, responding rapidly to amino acids in the water (Hodgson & Brown 1987) although exactly how food can be located even by this means is unknown. Any chemical gradient that nassariids are thought to need to successfully arrive at carrion (or its prey in the case of *P. incei*) (Britton & Morton 1994) is likely destroyed by the turbulence created by wave action. In this context, however, *P. incei* is probably a more efficient predator than *B. digitalis* is a scavenger, because in the latter species its food, carrion, is randomly moved by waves whereas in the former, unless migrating, the *Donax deltoides* prey is internally resident. Further, since the *P. incei* examined in this study were actively hunting their prey up shore, at or just above the region of maximum wave reach, it seems possible that *D. deltoides* juveniles are not so readily migratory as their adult conspecifics. Kitching & Pearson (1981) make the interesting observation that *P. incei* may detect its prey by sound or, more likely, the sound vibrations made as the bivalve moves in the sand. This might explain why *P. incei* hunts high on the shore above wave reach as the swash and backwash would mask any such vibrations. That is, within the waves any such minute vibrations would be undetectable. Numerous cases of *P. incei* in close association with *D. deltoides* juveniles lying on the sand surface were recorded for both Blue Lake Beach and One Mile Beach (Table 4) and on one occasion a bivalve was seen leaping to escape from a pursuing predator. Laws & Laws (1972) record that the mesodesmatid *Donacilla augusta* [= *Paphies elongata* (Reeve, 1854)] emerges from the sand in shallow subtidal water to avoid capture when *Polinices conicus* approaches it, and then reburrows once the predator has passed. Significantly, the five examples of *P. incei* drilling its captured prey were all identified lower down the shore, in the surf during low tide periods.

It thus appears that *Polinices incei* hunts *Donax deltoides* juveniles either close to, or at the sediment surface, high on the drying shore, and a captured prey (up to three individuals) is held at the rear of the foot and taken downshore where manipulation and drilling occurs within the substratum. The olive *Oliva tigridella* Duclos, 1835, that occupies low intertidal sand flats in eastern Australia also carries its prey, typically bivalves and gastropods, on the rear of its foot before consuming them later (Taylor & Glover 2000). Ansell & Morton (1987) also showed that *Polinices tumidus* Swainson, 1840, held its prey with the rear of its foot and, as a consequence, sometimes suffocated it such that there were no drill holes to identify the predation event. A similar observation was made upon *P. tumidus* by Vermeij (1980), that is, ~30% of the bivalve prey consumed by this predator in the laboratory showed no signs of drilling activity. It is thus significant that the prey individuals of *Donax deltoides* being held orally and drilled by *P. incei*, ranged in shell length from 15.2–29.5 mm, whereas those being held in the foot ranged in shell length from 3.1–15.8 mm. That is, there was little overlap between the two categories of prey. Although as this study shows there is a positive correlation between prey shell length and predator shell width, it would be very difficult to identify drilled shells of the *D. deltoides* juveniles being captured and held by *P. incei* in the beach sands. The smallest empty drilled individual of *D. deltoides* collected from One Mile Beach had a shell length of 15.0 mm. Sieving the beach sands might reveal if small individuals of *D. deltoides* are drilled post capture by *P. incei*. Further, it is unknown at what size and age *P. incei* commences drilling, although Wiltse (1980) has demonstrated that the larvae of *Polinices duplicatus* settle in close proximity to populations of its bivalve prey *Gemma gemma* and commence feeding soon after metamorphosis into juveniles occurs. Morton &
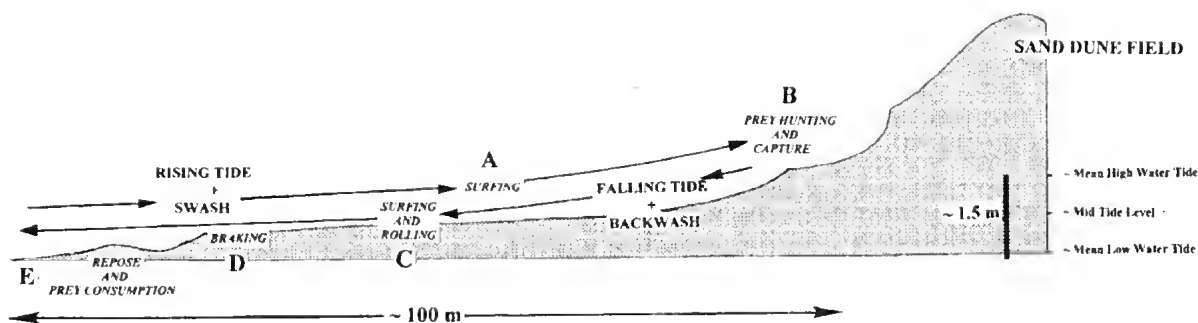
FIG. 16. A diagrammatic illustration of the profiles of the wave-exposed beaches on North Stradbroke Island and Port Stephens. The diagram also identifies aspects of the behaviour of *Polinices incei* that enable it to **A**, surf up the shore, and **B**, hunt and capture juvenile *Donax deltoides* in the swash of rising tides and return downshore by **C**, surfing and rolling, **D**, braking and burrowing to **E**, finally repose and consume its captured prey in the backwash of falling tides.

Chan (1997) similarly showed that newly settled juveniles of the nassariid *Nassarius festivus* (Powys, 1835) could also drill. More significantly, however, Ansell (1982) was able to maintain cultures of *Polinices catena* (da Costa, 1778) and hence plot juvenile rates of predation and growth. Juvenile *P. catena* ate approximately one hatchery-provided juvenile *Venerupis decussata* (Linnaeus, 1758) each day, and it does not seem unreasonable to suggest that *P. incei* would have a similar predation rate. Ansell (1982) also showed that as *P. catena* grew, so the size of prey needed also increased. This is reflected in the observations recorded herein for *P. incei* that in the field larger predators attacked larger prey *D. deltoides*. The largest *D. deltoides* observed being drilled (by a *P. incei* of 22.3 mm shell width) had a shell length of 29.5 mm (Table 5). The largest drilled (by an unknown naticid) valve of *D. deltoides* collected from Blue Lake Beach had a length of 38.6 mm. The largest *P. incei* collected had a shell width of 29.3 mm and it would thus seem reasonable to suggest that this individual (extrapolating Fig. 11) could have predated a *D. deltoides* individual of 38.6 mm shell length. That is, *P. incei* seems to be the only naticid present on the eastern Australian wave exposed shores and that its principal prey is *D. deltoides* juveniles up to a shell of ~39.0 mm. It is presumably unable to catch, handle or penetrate larger *D. deltoides* individuals and, thus, at shell lengths > ~39.0 mm the bivalve enters a size refuge from predation. This may help explain the unusual *D. deltoides* population

histogram (Fig. 2) where the largest (oldest) individuals comprise the dominant cohort. Such a surprising situation is, however, made more remarkable by the conclusion that *P. incei* preys, possibly exclusively, on a surf clam living in a habitat which has hitherto been regarded as a haven from predation.

Figure 16 is a diagrammatic illustration of the profiles of the wave-exposed beaches on North Stradbroke Island and Port Stephens. The average tidal range on such beaches is but ~ 1.5 metres so that waves become the dominant factor effecting not just the structure of the shore, but also in extending the tidal zone much further upwards than the limits exposed by the tides. The shores are thus about 100 metres from top to bottom. Fig. 16 also identifies generalised aspects of the behaviour of *Polinices incei* that enable it to A) surf up the shores, and B) hunt and capture juvenile *Donax deltoides* residing at their highest. This is undertaken in the swash of rising tides. Return down shore by *P. incei* with captured *D. deltoides* held by the foot is by C) surfing and rolling, and D) braking, and is undertaken in the backwash of falling tides. Over low tide periods *P. incei* individuals burrow into the sediment to E) find repose and drill and consume their captured prey.

Although nothing is known of the physiology of *Polinices incei*, clues can be obtained from the comprehensive research undertaken on the similarly surfing *Bullia digitalis* in South Africa by A.C. Brown and his co-workers. Brown (1971) has studied the ecology of *B. digitalis* and

shown (Brown 1979) that transport in the surf is, surprisingly, similar energetically in terms of oxygen uptake (1250 μg. hr⁻¹) to burrowing (1126 μg. hr¹), whereas crawling is much less (680 μg. hr¹). Thus, since once inflated, *P. incei* would (if it has a similar physiology to *B. digitalis*) not be spending any energy surfing, the increased energy required for such an activity must be related to the mechanism of inflation. Morris (1950) showed that inflation of the foot of the Australian naticid *Polinices strangei* (Reeve, 1855) was by a combination of muscular activity co-ordinated with the hydraulic pumping of blood into it. This creates a solid leading edge to the foot and a propodium shielding the front of the shell, as in all naticids, and which allows them to burrow in search of prey. In *Polinices incei*, however, such inflation, for the purposes of 'surfing' (or swash-riding) or crawling subsequent to 'braking', is extremely fast and must represent a possibly unique adaptation to the habitat it occupies and the prey it targets on such beaches. This is because the prey of naticids is not chosen randomly. Rather, there is a high degree of predator selectivity with respect to prey species and size — both absolute and relatively, according to predator size.

Such selective behaviour by naticids appears to be stereotypical, and has evolved over time, as evidenced by an inability to select novel prey under laboratory conditions (Boggs *et al.* 1984). Kitchell *et al.* (1981) have shown that prey selection by naticids is consistent with the concept and predictions of cost-benefit analysis, that is, optimal foraging theory (Hughes 1980) and its subsequent modification (Hughes & Dunkin 1984; Hughes & Drewett 1985). It is thus clear that *Polinices incei* has evolved to attack the surf clam *Donax deltoides* specifically. Donacids, it has been argued (Ansell 1981, 1983), have evolved to occupy highly dynamic surf beaches as, in part, a refuge from marine predators. As a result, donacids have generally escaped from naticid predation. The literature identifies only three examples of predation upon donacids. The first, by Ansell & Morton (1987) demonstrated that *Polinices tumidus* was able to feed on *Donax faba* (Gmelin, 1791) in laboratory experiments although the two do not naturally share the same habitat. The second by Vignali & Galleni (1987) suggested that strandline shells of *Donax semistriata* Poli, 1795, and *Donax trunculus* Linnaeus 1758, had been drilled by a naticid but with no proof. The third, by Negus (1975) only showed that strandline collected *Donax vittatus* (da Costa, 1778) had been drilled by a naticid, presumably offshore. In the highly dynamic habitat of wave-exposed beaches in eastern Australia, however, *Polinices incei* has evolved a remarkable suite of adaptations to follow and attack its chosen prey in a perceived sanctuary. In so doing, this remarkable predator not only broadens our picture of naticid adaptive radiation but also provides a remarkable example of the evolutionary 'arms race' that must constitute the selective force that has forged such a predator-prey relationship.

In the arms race that exists between predator and prey (Vermeij 1978), *Corbula crassa* Hinds, 1843, successfully defends itself against naticid attack by developing proteinaceous layers in the usual calcite of its shell (Morton 1990b), although in the Miocene of Poland *Corbula gibba* (Olivi, 1792) was readily attacked by two naticids — *Natica tigrina* (Röding, 1798) and *Hinia restitutiana* Fontannes, 1879 (Zlotnik 2001). The evolution of naticid drilling predation is part of the Mesozoic Marine Revolution (Vermeij 1977) entailing, especially in the tropics, the diversification of infaunal bivalve and other prey resources. As predicted by escalation theory, the dangers to such infaunal residents from naticid predation (especially following the family's diversification in the Cenozoic) seems to have increased over time, albeit via a complex pathway mediated by abiotic events linked to mass extinctions (Kelley & Hansen 2003). Since shallow water benthic assemblages are believed to be particularly susceptible to mass extinction events (Jablonski & Valentine 1981), it seems probable that the *Polinices incei/Donax deltoides* relationship is relatively modern. Notwithstanding, the relationship identified herein is a remarkable, and hitherto unrealised, example of predatory adaptive radiation.

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The biology of sympatric species of *Scintillona* (Bivalvia: Galeommatoidea) commensal with *Pilumnopeus serratifrons* (Crustacea: Decapoda) in Moreton Bay, Queensland, Australia, with a description of a new species

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ABSTRACT

Two species of the galeommatid genus *Scintillona*, *S. cryptozoica* and *S. daviei* sp. nov. are sympatrically associated with the gallery-building pilumnid crab *Pilumnopeus serratifrons* inhabiting clumps of the mussel *Trichomya hirsuta* on a seagrass-covered intertidal mudflat at Myora Springs, North Stradbroke Island, Queensland, Australia. The new species is described and compared with *S. cryptozoica*. Sympatry is not total: of the 100 galeommatid clusters examined, 40 of *S. cryptozoica* and 27 of *S. daviei* were species specific, and 33 were sympatric. Clusters of *S. cryptozoica* and *S. daviei* ranged in numbers from 1–25 and 1–7 individuals, respectively. Both species appear to be protandric consecutive hermaphrodites: the male component of the ovotestis dominated at shell length sizes of 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively; females ranged in shell length from 5–10 mm and 3–7.5 mm, respectively. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm. The relationship of both species with their host crab appears to be related to protection within its gallery and the provision of respiratory and feeding currents by virtue of its activities, and can thus be defined as commensalism. ❏ *Scintillona* species, *Galeommatoidea*, sympatry, *Pilumnopeus serratifrons*, Pilumnidae, biology, commensal relationship.

Fourteen species of mangroves occur in southeastern Queensland (Duke 2006), though only seven reach as far south as Moreton Bay, which is the southern limit for most species (Davie 1998). At Myora Springs on the northwest coast of North Stradbroke Island, the coastal fringe of mangroves mostly comprising *Avicennia marina*, *Aegiceras corniculatum* and *Rhizophora stylosa* gives way to an extensive area of mud that is colonised at mid-tidal levels by the seagrasses *Zostera capricorni*, *Halodule uninervis* and *Halophila ovalis*. As the tide recedes, the seagrass beds are seen to be dotted with clumps of the hairy mussel *Trichomya hirsuta* (Lamarck, 1819), up to ~15 cm in diameter. This large, up to 65 mm shell length, mussel has a wide distribution encompassing South Australia, Tasmania and New South Wales to as far north as northern Queensland (Lamprell & Healy 1998). The mussel clumps sit in shallow depressions in the mud, and when turned over, sometimes possess small groups of small, white, translucent bivalves. Two species of the genus *Scintillona* Finley, 1927 [formerly attributed to *Varotoga* (Iredale, 1931)]

(Galeommatoidea Gray, 1840) occur sympatrically beneath the mussel clumps. From the clumps have been recorded a number of other species of invertebrates, including an alpheid shrimp, but their bases are almost exclusively occupied by the pilumnid crab *Pilumnopeus serratifrons* (Kinahan, 1856). This crab creates galleries in its mussel clumps, and it is to the roofs of these that the two bivalves attach.

Scintillona cryptozoica (Hedley, 1917) has been recorded from New South Wales, but its sympatric congeneric is undescribed. This study is therefore a description of the new bivalve species as well as a study of the biology of the two species, including basic anatomy, the extent and intimacy of their sympatry, reproduction and the relationship with their host crab *Pilumnopeus serratifrons*.

The Galeommatoidea comprises a highly diverse group of miniature, commensal bivalves that are associated with an equally wide range of marine invertebrate hosts (Boss 1965a) (although *Cycladoconcha amboinensis* (Spärck, 1931) is possibly parasitic within the oesophagus of synaptid holothurians). Galeommatoids can also be members of quite complex communities, for example, the tiny (1.7 mm shell length) *Jousseaumiella concharum* shares a gastropod shell with a sipunculan and a polychaete (Knudsen 1944). They are, however, rarely recorded as associates of crabs although they do live with, similarly commensal, pinnotherids in often highly complex associations with larger invertebrate hosts (Manning & Morton 1987; Morton 1988). The association between the two species of *Scintillona* to be described herein with *Pilumnopeus serratifrons* is thus of especial interest, particularly with regard to their sympatry, the morphological adaptations they have, particularly of the mantle, and their expressions of sexuality that equip them for such a lifestyle.

Abbreviations. Institutions: Queensland Museum, Brisbane, Queensland (QM); Australian Museum, Sydney, New South Wales (AM); The Natural History Museum, London, UK. (NHM).

Shell and anatomical structures: A, Anus; AA, Anterior adductor muscle (or scar); ADT, Antero–dorsal tentacle; AT, Anterior tentacles; B, Byssal thread; DD, Digestive diverticula; ES, Exhalant siphon; F(H), 'Heel' of foot; F(T), 'Toe' of foot; H, Heart; HT, Hinge tooth; I, Intestine; ID, Inner demibranch; ILP, Inner labial palp; K, Kidney; L, Ligament; LP, Labial palp; OD, Outer demibranch; OLP, Outer labial palp; OVT, Ovotestis; PA, Posterior adductor muscle (or scar); PDT, Postero-dorsal tentacle; PS, Pigment spot; PT, Posterior tentacles; R, Rectum; RM, Reflected mantle; S, Socket; SUBC, Supra-branchial brood chamber; U, Umbo.

MATERIALS AND METHODS

From 9–24 February 2005, daily visits were made during periods of falling tides to the mud flats at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland. Here, the seagrass covered mud flats are dotted with byssally bound clumps of the mussel *Trichomya hirsuta*. On each visit, the clumps were picked up, turned over and examined for the galeommatid bivalves of the genus *Scintillona*. Where these were seen, all individuals were collected and put into pre-numbered vials of seawater. The clumps were then broken apart gently and any other animal species associated with the *Scintillona* individuals collected and placed in numbered tubes. On return to the laboratory, the *Scintillona* individuals were separated into species, that is, *S. cryptozoica* and a sympatric new species. Shell lengths of all individuals were measured. All individuals of all species collected in association with the mussel clumps, and the two species of *Scintillona* were identified to the highest taxonomic category.

Both *Scintillona* species were examined anatomically. Some individuals were drawn, others were dissected to expose details of shell and hinge structure, and general anatomy. The ciliary currents of the organs of the mantle cavity of both species were examined under a binocular microscope and elucidated using carmine dissolved in seawater. Finally, all individuals were sexed into one or other of four categories, that is: i) females brooding fertilised eggs in their ctenidia; ii) unfertilised females; iii) individuals of indeterminate sex; and iv) males. Subsequently, two individuals of the new species of *Scintillona* were, following routine processing and gold sputter coating, examined using a scanning electron microscope (Jeol 820) at the University of Cambridge.

Table 1. Data on the population structure of *Pilumnopeus serratifrons* inhabiting the mussel (*Trichomya hirsuta*) clumps on the shore at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland.

	Numbers	Mean carapace width (mm)	Range in carapace width (mm)	Nos of single individuals	Nos of M:F pairs	Nos of M:M pairs	Nos of F:F pairs
Males	45	7.3	3.5 – 14.5	32	5	4	1
Females	33	9.2	5.5 – 14.0	26	–	–	–
Gravid females	9 (of 33)	8.7	7.5 – 10.0	7	2	–	–

HABITAT NOTES

The clumps of *Trichomya hirsuta* have as their basis an empty oyster shell, *Saccostrea glomerata* (Gould, 1850), a valve of *Pinctada* cf. *fucata* (Gould, 1850), or *Isognomon ephippium* (Linnaeus, 1758) or that of a conspecific. The mussel clump so attached may comprise >30 individuals, and the hair-like periostracum that covers the posterior region of each individual's valves creates a matted covering to the byssally bound, compact mass. The bowl of mud in which each mussel clump sits, is not anaerobically black, but clearly aerated. When each mussel clump is turned over, typically the most obvious co-residents are the galeommatid bivalves. Other inhabitants of the galleries included the near ubiquitous occurrence of *Pilumnopeus serratifrons*, and either one or two individuals each of: i) *Alpheus* cf. *pacificus* Dana, 1852 (Caridea: Alpheidae); ii) *Phascolosoma* cf. *arcuatum* (Gray, 1828) and *P.* cf. *dunwichi* Edmonds, 1956 (Sipuncula); iii) *Paralepidonotus* cf. *ampulliferus* (Grube, 1878) (Annelida: Polynoidae); iv), *Favonigobius* cf. *lateralis* (Macleay, 1881) (Pisces: Gobiidae) and v) occasional representatives of four other species of Galeommatoidea (the latter all sent to Dr. P. Middlefart, Australian Museum, Sydney).

NOTES ON THE *PILUMNOPEUS SERRATIFRONS* POPULATION

A total of 78 individuals of *Pilumnopeus serratifrons* was collected comprising 45 males (57.7%) and 33 females (42.%). Nine females were gravid (27.3%). The mean carapace widths of male and female individuals of *P. serratifrons* were 7.3 mm and 9.2 mm, respectively. Interestingly, although all collected individuals were relatively small (ranging in carapace width from 3.5–14.5 mm), this species can reach about 28.0 mm in carapace width (Davie 1989). However, much of the material recorded by Davie (1989: 130) in his taxonomic revision of the species was of similar size to that recorded here. It would seem possible that smaller individuals preferentially inhabit mussel clumps as well as other narrow cavities such as in rotting logs and amongst oysters (Davie, pers. comm.). The broader habitat of this species is 'in the lower estuary or on sandy mud flats, living under stones and debris resting on the substrate, from about half tide level to low water' (Davie 1989).

The majority of individuals (32 males and 26 females occurred singly, although five male/female, four male/male and one female/female pairs were identified. Of the nine gravid (egg bearing) individuals collected, seven occurred singly while two were partners in the male/female pairs (Table 1). Morton & Lutzen (2008) report upon the rhizocephalan *Loxothylacus spinulosus* Boschma, 1928, parasitising *P. serratifrons* in the *Trichomya* clumps.

TAXONOMY

Hedley (1917, pl. xvi, fig. 1[animal]; pl. ii, fig. 40 [shell]) erected a new name, *Solecardia cryptozoica*, for a gregarious galeommatid species that lives in 'companies of a dozen or so' (p. 685) individuals underneath stones at low water in Middle Harbour, Sydney. Iredale (1931: 206) proposed the generic name *Varotoga* for this species, as he felt *Solecardia* was being too broadly used 'for any glassy oval shell'. Subsequently, Iredale (1936) described a second galeommatid occupying the burrows of the prawn *Crangon* from Bottle and Glass Rocks, Watson's Bay, Sydney. This was called *Ambuscintilla praeminum* gen. nov., sp. nov., although the illustration (pl. xxi, fig. 4) is clearly identical with that of

Varotoga cryptozoica (Hedley, 1917, pl. ii, fig. 40). Dr P. Middelfart (pers. comm.) believes that Iredale probably did collect specimens of a new species (of *Varotoga*) but that he also appears to have mixed them with at least one specimen of *V. cryptozoica* which was used for the published figure. As the deposited type specimen in the Australian Museum also belongs to *V. cryptozoica*, *Ambuscintilla praemium* must be treated as a junior synonym of *V. cryptozoica*.

Under current usage, *Varatoga* is considered a junior synonym of *Scintillona* Finlay, 1927 (see Lamprell & Healy 1998: 152). Dr Peter Middelfart is currently undertaking a revision of the Galeommatidea, and believes there are good reasons to maintain *Varatoga* as a separate taxon. However, until his revision is published it seems more appropriate to use *Scintillona* for the present work.

GALEOMMATOIDEA Gray, 1840
Galeommatidae Gray, 1840

Scintillona Finlay, 1927

Scintillona Finlay, 1927: 465 [type species: *Spaniorinus zealandica* Odhner, 1924].

Scintillona daviei sp. nov.
(Figs 1, 2, 3, 4, 5 & 6)

Material Examined. HOLOTYPE: QM-MO77617, shell length 4.5 mm, sand flat in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, 9–24,02, 2005, B. Morton. PARATYPES: QM-MO77618, shell length 4.0 mm, AM-C.454645, shell length 5.0 mm, AM-C.454646, shell length 5.0 mm, NHM 20060145, shell length 4.0 mm, NHM 20060146, shell length 4.5 mm, data as for holotype.

Etymology. The species is named after Peter Davie, Senior Curator (Crustacea), Queensland Centre for Biodiversity, Queensland Museum, Brisbane, Queensland, Australia, in gratitude for his endeavours in organising the workshop during which the material was collected.

Description. Small (< 7.5 mm shell length), approx. equilateral and equivalved. Holotype: shell 4.5 mm in length; almost as tall (4.0 mm) as long and laterally plump. Posterior valve face more inflated and pointed than the more marginally rounded anterior. Hinge line purple with an internal opisthodetic ligament and small anterior hinge teeth on both valves interlocking in a medial socket. Shell translucent with purple hinge.

Remarks. *Scintillona daviei* sp. nov. has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 1). The mantle margin is dark red around the exhalant siphon and yellow/orange around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. There are two pairs of other tentacles anteriorly and one pair posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red/purple apically. Such an arrange-

FIG. 1. *Scintillona daviei* sp. nov.: holotype (QM-MO77617) illustrated in life from the left side.

Table 2. *Scintillona cryptozoica* and *Scintillona daviei*: a comparison of anatomical characters.

Character	*Scintillona cryptozoica*	*Scintillona daviei*
Maximum shell length	10.0 mm	7.5 mm
Shell length to height ratio	1 : 0.69	1 : 0.75
Hinge area	Translucent white	Purple
Hinge teeth	Single anterior tooth in left valve	Single anterior teeth in left and right valves
Anterior tentacle area	Anterior tentacle red plus two other pairs	Anterior tentacle purple/red plus three other pairs
Posterior tentacle area	Posterior tentacle red plus thee other pairs	Posterior tentacle purple/red plus two other pairs
General mantle papillae	Numerous: scattered all over reflected mantle	Reflected mantle with inner ring of 12 pairs plus outer postero-ventral ring of five pairs
Pedal pigment spot	Absent	Present
Shell length of mature females	Females mature at > 5 mm	Females mature at > 3 mm

ment of tentacles and the purple hinge identifies the species.

According to Lamprell and Healy (1998) two species of *Scintillona* occur in Australian waters. These are *S. hyalina* (Deshayes, 1856) and *S. cryptozoica* (Hedley, 1917). The former is known only from the holotype in the collections of the Natural History Museum, London (BMNH 196791) and was collected in the Torres Strait but from an unknown habitat (see Lamprell and Healy, 1998, fig. 395). It is 14 mm long, equilateral and is elongately oval with a straight hinge line. It is clearly different from the much smaller, rounded, plump *S. daviei* sp. nov.

Scintillona daviei also differs from the only other known Australian species, *S. cryptozoica* (but with which it is sympatric, as this study will show), in a number of distinctive ways (Table 2). Firstly, not only is *S. daviei* smaller (<7.5 mm shell length) than *S. cryptozoica* (10 mm shell length), but it is also plumper, that is, the shell length to height ratio is 1:0.75, versus 1:0.69. Secondly, the hinge line and plate of *S. daviei* is always a distinctive purple and the arrangement of the hinge teeth between the two species is subtly different. There are, thirdly, distinctive differences in the arrangement of the tentacles and pallial papillae, but *S. daviei* also possesses a distinctive pigment spot in the

foot whereas *S. cryptozoica* does not. Differences between the species are further detailed more extensively under the headings 'Shell Structure and Anatomy' following.

Distribution. Known only from the type locality; sand flats in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, Australia.

SHELL STRUCTURE AND ANATOMY OF *SCINTILLONA DAVIEI*

The shell of *Scintillona daviei* sp. nov. is illustrated as a SEM image from the left side in Fig. 2A. It is translucent and covered in a thin (2 μm) periostracum. The umbo is tall and prosogyrous. The posterior face is more inflated and pointed than the narrower and more rounded anterior. Nevertheless, the species is approx. equilateral and equivalve. Internally (Fig. 3A), the anterior (AA) and posterior adductor (PA) muscles are of approximately equal sizes and are situated below the anterior and posterior hinge lines, respectively. The purple hinge plate is illustrated in Figs 2B, C and 3B, C. The ligament (Fig. 3, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve (Figs 2B & 3B). There is a similar hinge tooth in the right valve (Figs 2C, 3C, HT) and both abut each other but do not
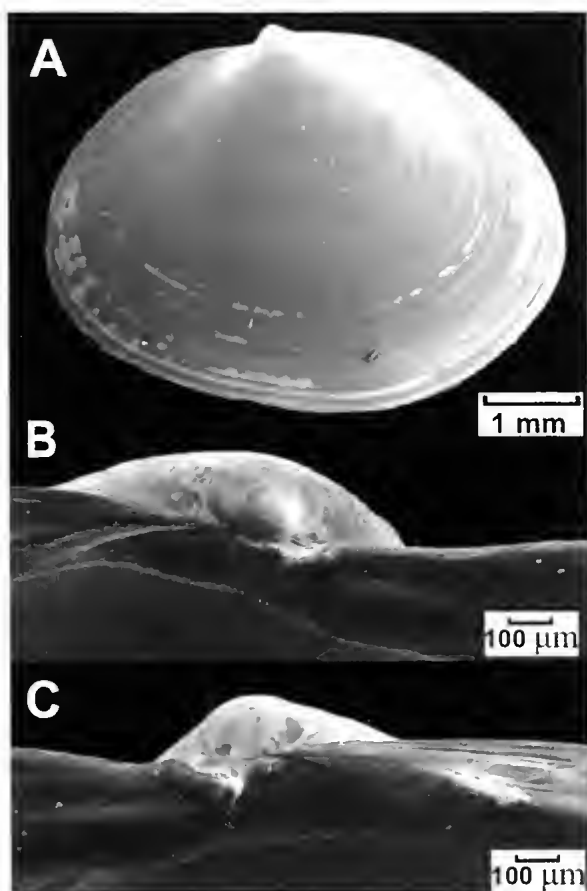
FIG. 2. *Scintillona daviei* sp. nov.: scanning electron micrographs of **A**, the external surface of the left shell valve; **B, C**, the internal structures of the left and right hinge plates, respectively.

FIG. 3. *Scintillona daviei* sp. nov.: **A**, internal view of the left shell valve; **B, C**, internal views of the left and right hinge plates respectively (see Abbreviations section earlier).

interlock. There is a medial socket (S) directly beneath the umbo.

A mature individual of *Scintillona daviei* is illustrated in life position in Fig. 4. The shell, as described above, is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). The outer surface of this fold is actually the inner (because the fold as a whole is reflected) and possesses a number of tentacles and papillae. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points of this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located
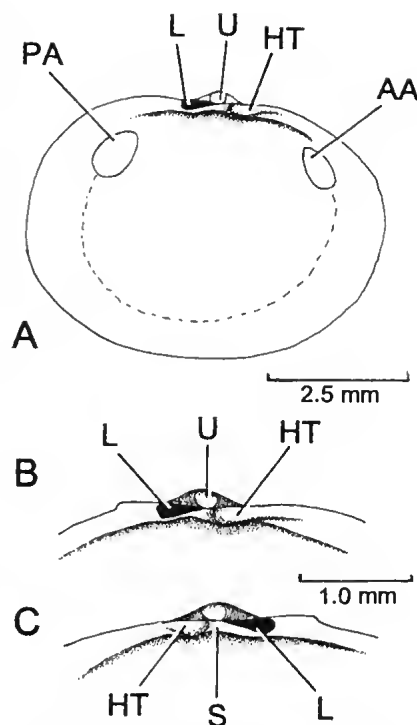
beneath the posterior dorsal tentacle (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are three pairs of anterior tentacles (AT) whereas posteriorly there is only one pair (PT). The outer surface of the mantle is adorned by two cycles of papillae above each valve. The outermost cycle approximately tracks the location of the postero-ventral valve margins. The inner cycle defines the mantle edge apically. Also seen in Fig. 4 is the extended foot, comprising a posterior 'heel' (F(H)) and a much longer anterior 'toe' (F(T)) within which is a distinctive red pigment spot (PS). The foot allows *S. daviei* to crawl effectively.

The anatomies of the organs of the mantle cavity of *Scintillona daviei* are illustrated from the left side in Fig. 5. Once again, the inhalant flow is indicated by closed arrows and the exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest struc-
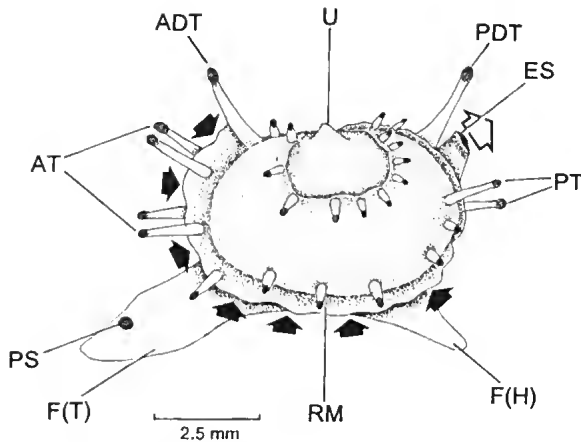
FIG. 4. *Scintillona daviei* sp. nov: individual illustrated from the left side showing the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).
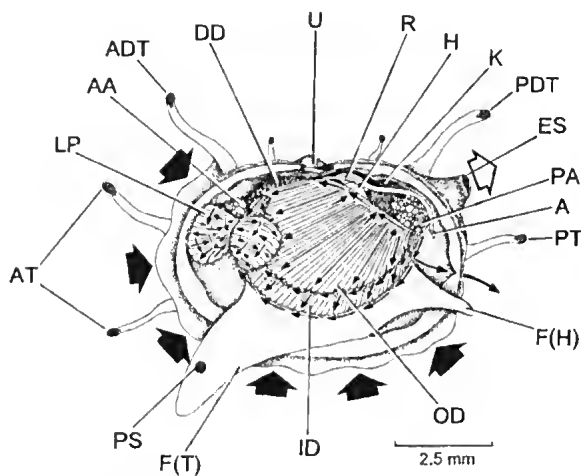

FIG. 5. *Scintillona daviei* sp. nov: structure and ciliary currents of the ctenidia and labial palps, as seen from the left side. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

tures in the mantle cavity and each comprises an inner (ID) and an outer demibranch. The pattern of ciliation on the ctenidia is of type C(1) (Atkins 1937) and thus bears a close resemblance to those of *Galeomma turtoni* (Sowerby, 1825) (Popham 1940), *Divariscintilla maoria* Powell, 1932 (Judd 1971) and *Galeomma takii* (Kuroda, 1945) (Morton 1973a). That is, only the inner demibranch bears a ventral marginal
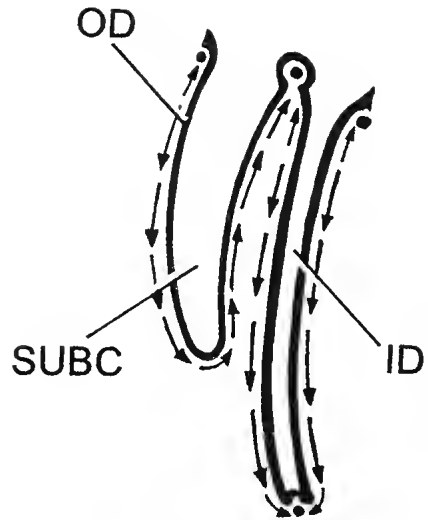

FIG. 6. *Scintillona daviei* sp. nov: diagrammatic transverse section through the right ctenidium showing the ciliary currents and the oral-ward currents (●) (see Abbreviations section earlier).

food groove, although there are other oralward currents in the ctenidial axis and where the ascending lamellae of the inner and outer demibranchs unite with the visceral mass and mantle, respectively. The outer demibranch does not achieve anterior contact with the labial palps. Rather, accepted material passes onto the inner demibranch to be transported to the labial palps. Such a ctenidial-labial palp configuration is typical of the Galeommatoidea and is of Category 3 (Stasek 1964). The labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles. Rejected material is evicted as pseudofaeces from the infra-branchial chamber of the mantle cavity posteriorly below the exhalant siphon (ES).

The structure and ciliation of the left ctenidium of *Scintillona daviei* are illustrated in transverse section in Fig. 6. The outer demibranch (OD) only, enclosing this component of the supra-branchial chamber (SBC) is modified for the brooding of fertilised eggs and larvae. The longer inner demibranch (ID) is hence the main ciliary potential food transporting structure in *S. daviei*.
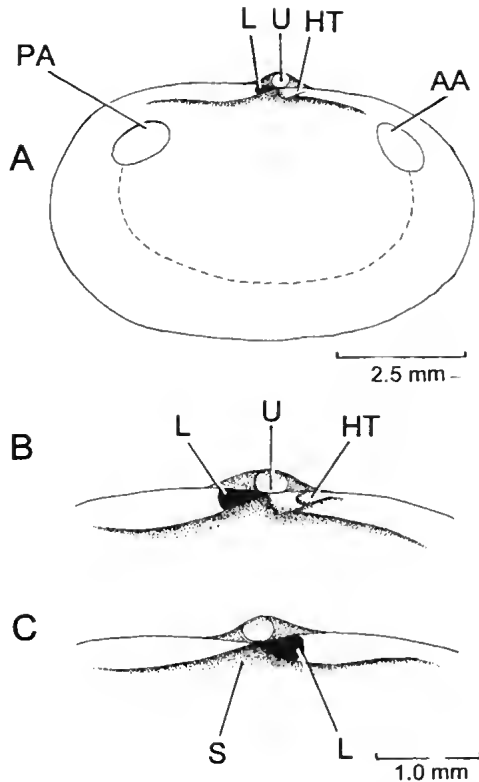
FIG. 7. *Scintillona cryptozoica*: **A**, internal view of the left shell valve; **B**, **C**, internal views of the left and right hinge plates, respectively (see Abbreviations section earlier).

SHELL STRUCTURE AND ANATOMY OF *SCINTILLONA CRYPTOZOICA*

The shell of *Scintillona cryptozoica* has a maximum length of 10 mm and is longer relative to shell height than *S. daviei*. The shell is uniformally translucent white and covered by a very thin (2 μm) periostracum. The shell is also more equilateral than *S. daviei* but is similarly equivalve. The internal structure of the shell is illustrated in Fig. 7A. The anterior (AA) and posterior adductor (PA) muscles are of approx. equal size and are situated below the anterior and posterior hinge lines, respectively. The hinge plate is illustrated in Fig. 7B & C. The ligament (Fig. 7, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve only (Fig. 7B). There is not a similar hinge tooth in the right valve as there is in *S. daviei*. There is, however, a medial socket (S) directly beneath the umbo.

A mature individual of *Scintillona cryptozoica* is illustrated in life position in Fig. 8. It is suspended by a single byssal thread (B) from the roof of the crab gallery in the mussel clump. The shell is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). As in *S. daviei*, the outer surface of this fold is actually the inner and possesses a number of tentacles and papillae all of which are tipped deep red. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points along this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located beneath the posterior dorsal tentacle (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are two (three in *S. daviei*) pairs of anterior tentacles (AT) whereas posteriorly there are four (only one in *S. daviei* sp nov.) pairs (PT). The outer surface of the mantle is adorned by an array of numerous papillae. Also seen in Fig. 8 is the posterior 'heel' of the foot (F(H)). The foot allows *S. cryptozoica* to crawl.

Scintillona cryptozoica, like *S. daviei*, has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 9). The mantle edge is a light red around the exhalant siphon and yellow around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. In addition, there are two pairs of other tentacles anteriorly and four pairs posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red apically. Such an arrangement of tentacles and papillae, the translucent hinge and the absence of a pigment spot in the foot of *S. cryptozoica*, distinguishes it from *S. daviei*.

The anatomies of the organs of the mantle cavity of *Scintillona cryptozoica* are illustrated from the left side in Fig. 10. Here, the inhalant flow is indicated by closed arrows and the
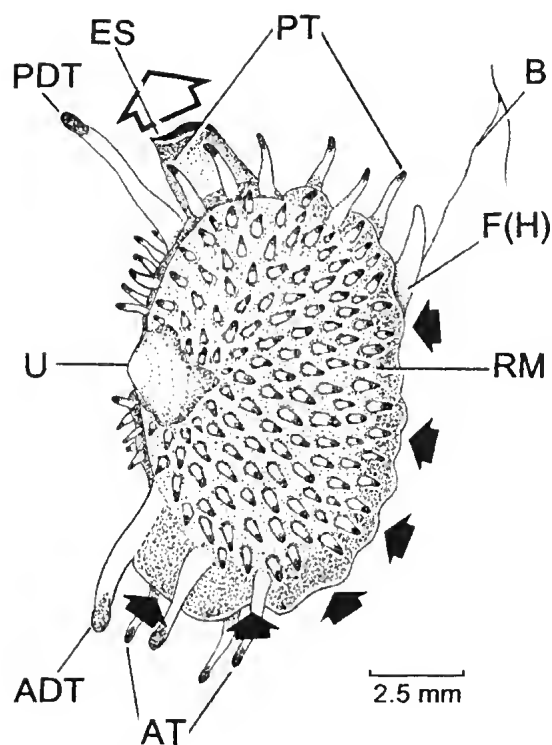
FIG. 8. *Scintillona cryptozoica* illustrated in life position attached to the roof of the gallery made by the crab *Pilumnopeus serratifrons* in the clump of *Trichomya hirsuta*. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest structures in the mantle cavity and each comprise an inner (ID) and an outer demibranch. The outer demibranch is much reduced in comparison with the inner, as in *S. daviei*. Similarly, the ctenidial-labial palp configuration is of Category 3 (Stasek 1964) and the labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles.

The ciliary currents of the inner surface of the mantle and the visceral mass of *Scintillona cryptozoica* are illustrated in Fig. 11. When viewed from the left side, the ciliary currents of the visceral mass move particles in an anticlockwise direction. That is, dorsally particles are moved by an oralward current that approximates the position of a similarly directed current in the junction of the ascending lamella of the inner demibranch with the visceral mass. Material is then circulated downwards and backwards, to eventually fall from the visceral mass posteriorly and be captured by the currents of the mantle. These move particles in a similar anticlockwise direction on the inner surface of the right mantle lobe (but of course in a clock-

FIG. 9. *Scintillona cryptozoica*: mature individual illustrated from the left side.
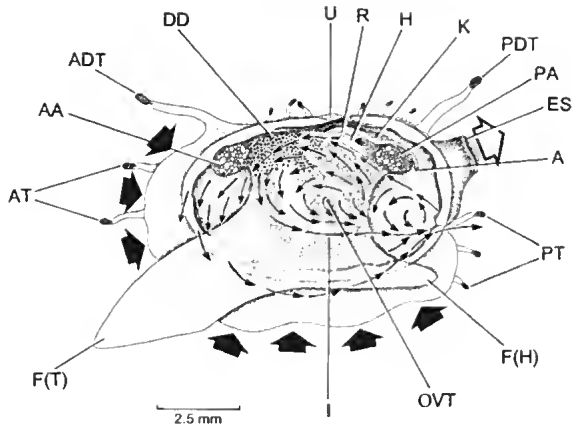
FIG. 10. *Scintillona cryptozoica*: organs and ciliary currents of the ctenidia and labial palps, as seen from the left side. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).
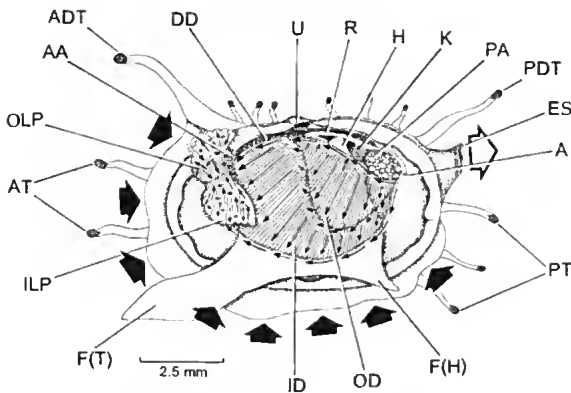

FIG. 11. *Scintillona cryptozoica*: organs and ciliary currents of the visceral mass. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

wise direction on the left) circulating material from the postero-dorsal region of the mantle cavity forwards but then backwards ventrally. When such a flow arrives posteriorly, held and other captured material rejected by the visceral mass, is discharged from the mantle cavity as pseudofaeces at a point just below the exhalant siphon.

POPULATION STRUCTURES OF *SCINTILLONA DAVIEI* AND *SCINTILLONA CRYPTOZOICA*

Of the 100 clusters of *Trichomya hirsuta* that possessed the commensal galeommatids, 40 com-

prised groups of only *Scintillona cryptozoica*, 27 comprised groups of *S. daviei* and 33 were sympatric. That is, the sympatry is neither 100% nor, obviously, obligatory. Clusters of *S. cryptozoica* and *S. daviei* contained numbers of individuals ranging from 1 to 25 and 1 to 7, respectively.

Figure 11 shows the position of the ovotestis (OVT) in the visceral mass of *Scintillona cryptozoica*. This has not been examined histologically, but it develops primarily postero-ventrally around the intestine (I). Both species appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females of the two species ranged in shell length from 5–10 mm and 3–7.5 mm, again respectively. Both species brood fertilised eggs in the outer demibranchs only of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm (Fig. 12). It seems that in both *S. cryptozoica* and *S. daviei*, the colour (and its intensity) of the tips of the mantle tentacles and papillae change (and are enhanced with size which is also related to both age and stage of sexual development (Table 3).

The compositions of the clusters of *Scintillona cryptozoica* are identified in Table 4. Cluster composition ranged from solitary individuals (x 23) to 25 individuals (x 1). Most individuals were thus in clusters of more than one and an average of 8.7. Solitary individuals comprised but 8.2% of the total population and most of these (16) were in the intersex stage. Significantly, brooding females were never solitary and were recorded from clusters comprising 2, 9 and 14 individuals. That is, they are associated with one or more males which are presumably required to effect fertilisation. The greatest numbers of individuals in the clusters were at the intersex stage and, except for one case of clusters of 14 individuals, these always out-numbered females by a factor of > 2:1 and more often by ~ 6:1. That is, each cluster of more than one individual of *S. cryptozoica* usually comprised a female plus a number (1–6) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster there was also usually a male present. Thus, of the total of 73 clusters of *S. cryptozoica* examined, the average

Table 3. Variations in colour with size in *Scintillona cryptozoica* and *Scintillona daviei*.

Reproductive stage	~Shell length range (mm)	*Scintillona cryptozoica*	~Shell length range (mm)	*Scintillona daviei*
Male	1.0–3.0	Both tentacles pale	1.0–2.5	Both tentacles very pale
Intersex	2.0–8.5	Both tentacles pale yellow	2.0–6.0	Both tentacles pale red/purple
Female	5.0–10.0	Posterior tentacle red: anterior paler	3.0–7.5	Posterior tentacle red/purple: anterior paler
Brooding female	6.5–8.0	Both tentacles bright red	3.5–6.0	Both tentacles bright red/purple

Table 4. The composition of the clusters of *Scintillona cryptozoica*.

Cluster size (Nos of individuals)	1	2	3	4	5	6	7	8	9	11	14	18	25	
Numbers of such clusters	23	14	9	7	4	1	2	5	1	1	4	1	1	
Total no. individuals	23	28	27	28	20	6	14	40	9	11	56	18	25	
Cluster composition														
Male	1	2	3	3	–	–	–	1	1	–	5	2	4	22
Intersex	16	14	16	20	17	6	10	33	5	8	15	16	18	194
Female	6	7	8	5	3	–	4	6	2	3	33	–	3	80
Brooding females	–	5	–	–	–	–	–	–	1	–	3	–	–	9

Table 5. The composition of the clusters of *Scintillona daviei* sp. nov.

Cluster size (Nos of individuals)	1	2	3	4	5	6	7	
Numbers of such clusters	23	12	11	5	5	2	1	
Total numbers of individuals	23	24	33	20	25	12	7	
Cluster composition								
Male	3	1	1	–	2	3	–	10
Intersex	12	9	25	10	15	5	7	83
Female	7	7	4	9	3	3	–	33
Brooding females	1	7	3	1	5	1	–	18

cluster of between 8–9 individuals comprised a ratio of 0.30 males: 2.66 intersex individuals: 1.09 females and 0.12 brooding females.

The compositions of the clusters of *Scintillona daviei* are identified in Table 5. Cluster composition ranged from solitary individuals (x 23) to 7 individuals (x 1). Most individuals (61%) were thus in clusters of more than one and an average of 4. Solitary individuals comprised 16.0% of the total population and most of these (12: 52.2%) were in the intersex stage. Brooding females were never solitary and were recorded from clusters comprising 1–6, but not 7 individuals. Similarly, all cluster sizes, save those comprising 4 and 7 individuals, possessed at least one male. That is, one or more males was always associated with clusters containing mature and brooding females, suggesting, as for *S. cryptozoica*, that a male is required for fertilisation. Also as for *S. cryptozoica*, the greatest numbers of individuals (83: 57.6%) in the clusters were at the intersex stage and always outnumbered

females by an average factor of 2.5:1 and males by often ~8:1. That is, each average cluster of more than one individual usually comprised a female plus a number (~3) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster then so was a male. Of the total of 59 clusters of *S. daviei* examined, therefore, the average cluster of four individuals comprised a ratio of 0.7 males: 0.58 intersex individuals: 0.23 females and 0.12 brooding females.

Both species of *Scintillona* thus appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of between 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females ranged in shell length from 5–10 mm and 3–7.5 mm for *S. cryptozoica* and *S. daviei*. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm, again respectively. It seems that the larvae incubated in the female outer demibranchs of both species of *Scintillona* are released as veligers and after an undefined period of time in the plankton, find a *Pilumnopeus serratifrons* host gallery in the mussel clumps. There, if a female is in residence, such newly settled juveniles become males. If a female is not present they seem to become of undefined sexuality or 'intersex' and may await, as they grow, further male discovery when they would become females. Fertilised females of both species were the largest individuals in the clusters and it seems possible that following successful brood hatching they die, allowing the next oldest intersex/putative female to mature. There is thus and, as would be expected in such a pattern of reproduction, a dominance in the clusters of both species by intersex/putative females.

DISCUSSION

The two species of *Scintillona* herein described and discussed are not only clearly closely related but also at least partially sympatric. Galeommatoidean bivalves are well known associates of marine invertebrates, being recorded from a wide range of phyla (Boss 1965a). Although all galeommatoideans are small as a consequence of their symbiotic lifestyles, species of the Galeommatidae show

great reduction of the shell valves and reflection of the middle fold of the mantle over them (Morton 1973a, 1975). Adoption of a mode of life that can typically best be defined as 'commensal', that is, benefiting from the respiratory currents of the host to facilitate respiration and suspension feeding (Morton 1988) has also been achieved by reproductive specialisation, e.g., the storage (Morton 1980; O'Foighil 1985) of dimorphic sperm (Jespersen *et al*. 2002); simultaneous and consecutive hermaphroditism (Gage 1968a); sexual dimorphism (Jenner & McCrary 1968); self fertilisation (O'Foighil 1987); and even dwarf males (Morton 1976, 1981). *Mysella tumida* (Carpenter, 1864) produces spermatophores to effect fertilisation (O'Foighil 1985), while Mikkelsen & Bieler (1992, fig. 33) described a form of mating behaviour in their new species *Divariscintilla octotentaculata*. *Turtonia minuta* (Fabricius, 1780) produces egg capsules (Oldfield 1963). In the absence of any facilities for histological sectioning of the two species of *Scintillona* here under consideration, it is unknown if sperm is
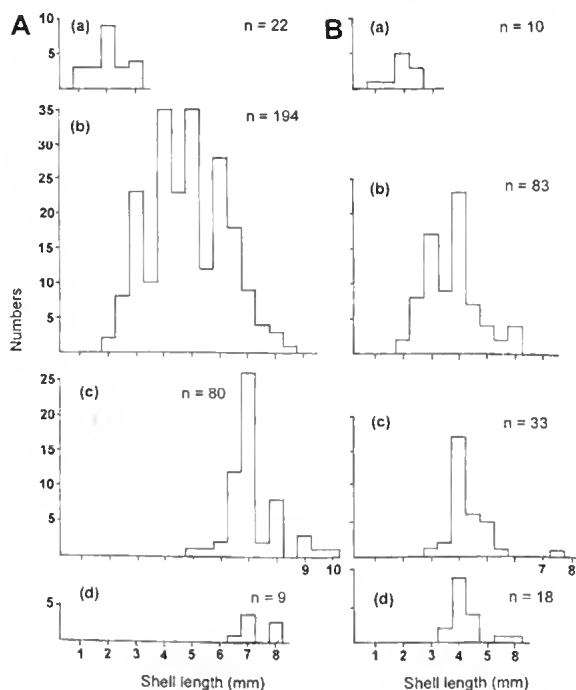

FIG. 12. Shell length histograms illustrating the population structures of: **A**, *Scintillona cryptozoica*; **B**, *S. daviei* sp. nov. (a) = males; (b) = intersex individuals; (c) = females; and (d) = brooding females.

either stored or is dimorphic: notwithstanding, both species appear to be consecutive protandric hermaphrodites, that is, with newly settled males attracted to females which are then fertilised to produce eggs that are incubated within the outer demibranchs. In two cases, two small males (shell lengths of ~1–1.5 mm) were identified (a) inside the mantle cavity and (b) attached to the byssus of females. Incubation is only to the D-veliger stage, however, no brooded crawl-away juveniles ever being seen.

The males of the two *Scintillona* species are thus not strictly 'dwarf' but probably, as proposed for *Pseudopythina subsinuata* (Lischke, 1871) by Morton (1972), will settle into a clump of adults and become male if an established, maturing female is resident. In the absence of a female, the newly settled individual may become a putative female. This results, as suggested for the present species (Fig. 12), in a surfeit of either putative or intersex females, with each cluster being optimally dominated by one or two mature, possibly gravid or brooding, females. With completion of their life spans, younger females can then assume their places in the cluster hierarchy. Such a pattern of protandric consecutive hermaphroditism has also been identified for *Lepton nitidum* Turton, 1822 (Pelseneer 1925), *Arthritica crassiformis* Powell, 1833 (Morton 1973b), *Montacuta elevata* (Stimpson, 1851) (Verrill & Bush 1898) Gage 1968a), *Mysella cuneata* (Gage, 1968b), *Montacutona compacta* (Gould, 1861) (Morton 1980).

The situation in *Scintillona cryptozoica* and *S. daviei* species most closely resembles that seen in *Pseudopythina rugifera* (Carpenter, 1864). O'Foighil (1985b) described 'temporary' dwarf males in *P. rugifera*, as was postulated for *P. subsinuata* by Morton (1972), with both authors providing histograms showing small males and larger females.

Morton & Scott (1989) reviewed the commensal, galeommatid bivalves of Hong Kong, identifying 22 species. Lützen & Nielsen (2005), however, recorded 27 species from intertidal reef flats at Phuket (Andaman Sea), Thailand, and over 50 species are known from Japan (Habe 1977, 1981). Very few, however, have been recorded as occurring with crabs. Manning & Morton (1987) reported upon *Frousella ohshimai* Habe, 1964 [=*Pseudopythina nodosa* (Morton & Scott, 1989)] and *Nipponomysella subtruncata* (Yokoyama, 1922) [=*Barrimysia siphonosomae* (Morton & Scott, 1989)] from Hong Kong living with pinnotherids in the burrows of sipunculan worms. Similarly, few galeommatids are recorded as being sympatric with their hosts. Notwithstanding, Morton & Scott (1989) showed that the shallow water holothurian *Protankyra bidentata* (Woodward & Barrett, 1858) may have three galeommatoideans resident with it in Hong Kong, that is, *Pseudopythina ariakensis* (Habe, 1959), *P. tsurumaru* (Habe, 1959) and *Entovalva semperi* Ohshima, 1930. Similarly, Mikklesen & Bieler (1992) reported upon six species of galeommatoiden bivalves, five of them species of *Divariscintilla* and *Parabornia squillina* Boss, 1965 (Boss 1965b), all living in the burrows of *Lysiosquilla scabricauda* (Lamarck, 1818) in eastern Florida. The five species of *Divariscintilla* were often collected together (see Mikklesen & Bieler 1992, p. 15 for a description) in a clearly complex sympatric relationship(s). Likewise, in Australian waters, three species of *Ephippodonta*, that is, *E. macdougalli* Tate, 1889, *E. lunata* Tate, 1889 and *E. turubullae* (Buick & Bowden, 1951), along with three other species of *Myllita*, that is, *M. tasmanica* Tenison-Woods, 1875, *M. gemmata* Tate, 1889 and *M. deshayesi* d'Orbigny & Recluz, 1850, as well as an un-named species of *Kellia* can all be found within the burrows of the mud-lobster *Strahlaxius plectrorhyncus* (Strahl, 1862) (Tate 1889; Matthews 1893; Woodward 1893; Cotton & Godfrey 1938; Buick & Bowden 1951). Finally, Lützen & Nielsen (2005) report that many of the 27 species of galeommatoideans they collected from reef flats in Phuket, Thailand, occurred in small (undefined) intra- and inter-specific family 'flocks'.

Although burrowing anomurans and stomatopods are favoured hosts of galeommatoideans (Boss 1965a; Mikkelsen & Bieler 1989, 1992), there are few reports of them being associated with crabs. Morton & Scott (1989) described *Pseudopythina macrophthalmuensis* Morton & Scott, 1989, attached to the limbs of the burrowing crab *Macrophthalmus latreillei* (Desmarest, 1817) in Hong Kong, whereas in Okinawa, Japan, it attaches to *M. convexus* Stimpson, 1858 (Kosuge & Itani 1994). Boyko & Mikkelsen (2002) describe *Mysella pedroana* Dall, 1899 attached to the spiny

(also burrowing) anomuran sand crab *Blephari-poda occidentalis* Randall, 1840, often inside the branchial chambers. It was initially suggested by Iredale (1936), that *Scintillona cryptozoica* lives in the burrows made by a species of '*Crangon*' (a species of pistol shrimp in the Alpheidae), however although an alpheid, *Alpheus* cf. *pacificus*, was twice collected from the mussel clumps herein examined, only the crab *Pilumnopeus serratifrons* was recorded within all the clumps, and it was this species that appeared to be creating the galleries to the roofs of which *S. cryptozoica* and *S. daviei* were attached.

Both species of *Scintillona* are similar to *Cerato-bornia cema* (Narchi, 1966) and *Divariscintilla yoyo* (Mikkelsen & Bieler, 1989) and other species of *Divariscintilla* (Mikkelsen & Bieler 1992), in that they hang by a solitary byssal thread from the roofs of the burrows they inhabit, in the latter cases *Callianassa major* Say, 1818, and the stomatopod *Lysiosquilla scabricauda*. The two species of *Scintillona* herein discussed also possess a complex pattern of large pallial tentacles. The function(s) of the large tentacles are, however, unknown. Such tentacles are absent in some galeommatoidean species, for example, *Scintilla stevensoni* Powell, 1932 (Ponder 1967: fig. 13). In *Rhamphidonta retifera* (Dall, 1899), there are single antero- and postero-dorsal tentacles (Bernard 1975, fig. 2). In the two species of *Galeomma* described by Morton (1973a, 1975), the dorsal tentacles are not only retractable but can autotomise and, in so doing, it was suggested, release a noxious secretion. The complex tentacles of the two species of *Scintillona* are neither retractable nor did they autotomise. Notwithstanding, as with the complex tentacles described for species of *Divariscintilla* Mikkelsen & Bieler (1989, 1992) and for *D. maoria* Powell, 1932, by Judd (1971), they are possibly defensive. That is, they may release a noxious secretion when touched to deter contact from other gallery inhabitants. It is, however, also interesting that the colours of the two species of *Scintillona* deepen with age, and it may be that they also secrete pheromones, as suggested for the yet more complex pallial tentacles of *Chlamy-doconcha orcutti* Dall, 1884, by Morton (1981), and in view of the suggestion by Mikkelsen & Bieler (1992) that *Divariscintilla octotentaculata* engages in a 'mating' behaviour.

Another interesting point is that galeommat-oideans living in close association with or upon crabs (see above), typically do not have a reflected mantle and hence no pallial tentacles. This is not true however for the two species of *Scintillona* herein discussed that live in galleries created and inhabited by *Pilumnopeus serratifrons*, and for their relatives identified above, that live attached to the burrows of anomurans (Boss 1965a). Thus, the possession or lack thereof of pallial tentacles is not wholly related to the category of host, that is, crustacean, worm or other taxon, but to the structure of the galleries or burrows the host creates.

Finally, it is of interest to speculate upon the nature of the relationship between the bivalves and *Pilumnopeus serratifrons*. As described above, the degree of sympatry between the two bivalves is not absolute and thus not obligate. However, the associations between the two bivalves with *P. serratifrons* do appear to be obligate, that is, they have never been recorded from clumps of *Trichomya hirsuta* without the crab (unless the crab escaped during handling, but still leaving a definable gallery behind). The bivalves clearly benefit from the protection, that is, aegism as defined by Morton (1988), afforded by living in a gallery underneath a *Trichomya* clump. However, the crab, by virtue of its activities, must aerate its gallery and, in so doing, bring in suspended particulates that the bivalves can exploit. Both species had such particulates in their mantle cavities and intestines. Grutter & Irving (2007) define such an association as facilitation or commensalism. Morton (1988) defines such an association, ident-ified for a number of similar galeommatoidean/host associations from Hong Kong, as commen-salism.

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Body posturing in *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* (Mollusca: Gastropoda: Littorinidae): a behavioural response to reduce heat stress

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ABSTRACT

Field observations on posture positions adopted by two species of littorinids, *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* in response to environmental temperatures were investigated. The study was conducted at a rocky shore of Hospital Bay, North Stradbroke Island, Queensland, Australia, from 19–22 February 2005. Temperature difference between rock surface and the outer surface of the snail shell was used as the response variable to test the hypothesis that posturing in the littorinids was a behavioural response to reduce heat stress. There was no significant interaction between 'species' and 'posture' in the two-way ANOVA results for the first two days' data; only 'posture' differed significantly in TempDiff (TempDiff$_{flat}$ < TempDiff$_{standing}$) but not for 'species'. Mean TempDiff for 'flat' and 'standing' postures, regardless of species, were 0.10 ± 0.61°C and 0.71 ± 0.89°C respectively. One additional posture was observed in *N. pyramidalis* on the third and fourth days: 'lifted' posture in which the opercular opening is closed and the shell slightly lifted off the rock surface but not entirely in the vertical/upright position. TempDiff for the three postures of *N. pyramidalis* was significantly different with TempDiff$_{lifted}$ ≈ TempDiff$_{flat}$ < TempDiff$_{standing}$ (Tukey's Test). Mean TempDiff for 'lifted', 'flat' and 'standing' postures for *N. pyramidalis* for the third and fourth days were –0.02 ± 0.67°C, 0.02 ± 0.52°C and 1.07 ± 0.73°C respectively. The 'standing' posture significantly reduced the temperature of the snails and is thus, an effective adaptive strategy in overcoming heat stress for these two species of littorinids. ❑ *marine, intertidal, snail, behaviour, heat stress, Queensland, Moreton Bay*

Supralittoral marine organisms of an intertidal rocky shore must endure the physical stress of temperature and salinity fluctuations and are highly susceptible to desiccation (Vermeij 1972; Underwood 1973; Newell 1979; Little & Kitching 1996; Raffaelli & Hawkins 1996; Lang *et al.* 1998). Mechanical wave action may also be intense (Minton & Gochfeld 2001). Survival on the high shore may be enhanced by a combination of morphological, physiological or behavioural adaptations.

One highly successful group in this harsh environment is the littorinid snails. Comparative studies of gastropod thermal tolerance have shown that members of the superfamily Littorinoidea are generally the most heat tolerant animals on rocky shores (Fraenkel 1966, 1968; Stirling 1982; Cleland and McMahon 1990; McMahon 1990; Britton 1992). McMahon (2001) reported that the mean heat coma temperatures of littorinoids were higher than that of six other high shore superfamilies of molluscs. Being mobile

also helps as they are able to select particular micro-habitats, such as pits and crevices, to alleviate thermal and desiccation stress (Garrity 1984; Britton 1992; Jones & Boulding 1999). Nevertheless, they are regularly subjected to prolonged sun and heat exposure when there is a lack of shelter.

How do these littorinids overcome such heat stress? The small species *Littorina striata* uses both its nodulose shell surface, and posture, to more effectively re-radiate absorbed incident radiant thermal energy by convection (Britton 1995). More typically, when ambient rock temperatures are too high or humidity is low, littorinids prevent desiccation by withdrawing into their shell and sealing the opercular opening. In addition, littorinids have been observed to attach themselves to the substratum by a dried mucous sheet at the outer apertural tip (termed a 'holdfast' by Bingham 1972) (see also Vermeij 1971a; Denny 1984; Garrity 1984; McMahon & Britton 1991; Wada & Ito 2000). The strength and stiffness of dehydrated mucous holdfasts (as little as 2–3 mm in thickness), allow littorinids to maintain their position with minimal effort while in repose (Denny 1984). One study found holdfast formation in *Littorina irrorata* to be dependent on relative humidity and salinity (Bingham 1972); while for *L. striata*, Britton (1995) observed that holdfasts were more frequently used by smaller individuals than larger ones.

More importantly, the holdfast minimises the area of contact between the gastropod and the heated substratum, reducing heat transfer by conduction (Vermeij 1971b). Vermeij (1971b) reasoned that a 'hanging' attachment increases the surface area exposed to convection currents and thus is more effective at removing heat; this is helped further if the gastropod is positioned under a shaded ledge as observed by Lang *et al.* (1998). Wada & Ito (2000) used an alternative term, 'tip-lip' attachment, as they observed *Nodilittorina radiata* more commonly using the holdfast on horizontal surfaces.

The term 'standing' is here used to describe the position in which the gastropod is held verti-
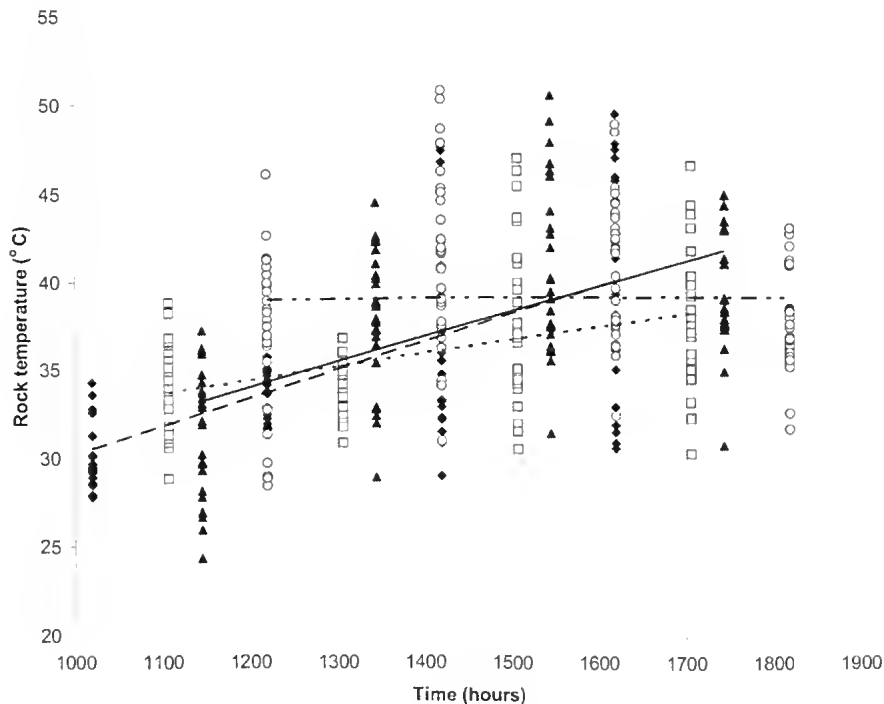

FIG. 1. Rock temperature profile taken at two-hour intervals for six-hour duration on the four consecutive days of 19–22 February 2005. First and last measurements were taken three hours before and after low tide respectively each day. ◆– – – 19 Feb.; □ ⋯⋯ 20 Feb.; ▲— 21 Feb.; ○– · · – 22 Feb.
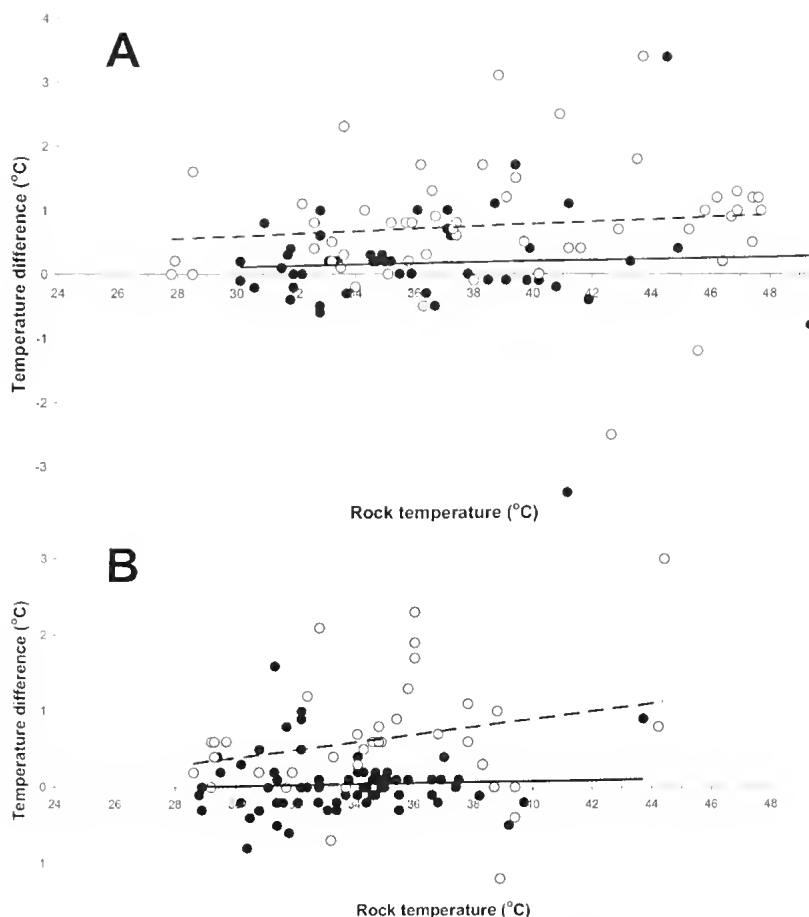
FIG. 2. Regressions of temperature difference between littorinid shell and rock surface against rock temperature for 'standing' and 'flat' postures in **A**, *Nodilittorina pyramidalis*; **B**, *Austrolittorina unifasciata*. ● = 'flat', ○ = 'standing'.

cally off the rock surface by its holdfast (Fig. 3A–C). During the present study *Nodilittorina pyramidalis* and *Austrolittorina unifasciata* were observed to exhibit this 'standing' posture, with it being more common in *N. pyramidalis*. This behaviour has not been previously documented for either species, and thus it was decided to test whether they are also using such a 'standing' posture as an effective strategy to reduce heat stress.

MATERIALS AND METHODS

This study was conducted at the intertidal rocky shore off Hospital Bay adjacent to the Moreton Bay Research Station, Dunwich, North Stradbroke Island, Queensland. It has focussed on two species of littorinids: the larger, but less

common *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833), and the smaller, more abundant *Austrolittorina unifasciata* (Gray, 1826) (Fig. 4A, B). Field work was carried out over four days from 19 to 22 February 2005, for six hours each day. The topography of the shore was such that rocks on which the littorinids were sampled are entirely submerged at high tide. These rocks are only uncovered by the receding tide about four hours prior to the lowest tide each day. Hence, the first set of temperature measurements was taken three hours before the lowest tide, with subsequent readings recorded at two-hourly intervals. The lowest tide each day occurred at 1322 hrs, 1402 hrs, 1446 hrs and 1521 hrs respectively. Four sets of temperature measurements were recorded daily. The surface temperatures of the
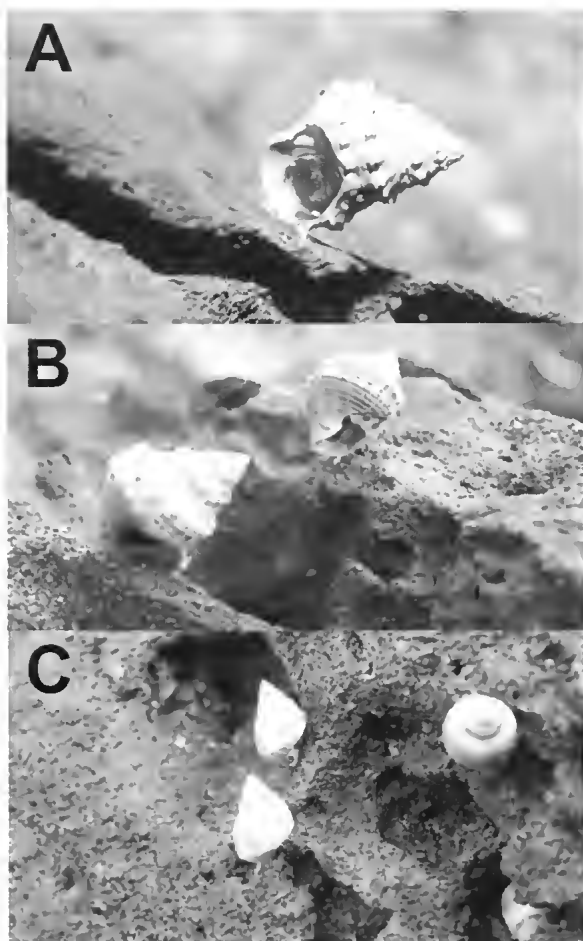
FIG. 3. **A**, thin holdfast of *Nodilittorina pyramidalis* securing it in the 'standing' posture; **B**, two individuals of *N. pyramidalis* in the 'standing' posture with spires pointing in the same direction; **C**, *Austrolittorina unifasciata* in the 'standing' position.

littorinid shells and the adjacent rock surface were measured (± 0.1°C) with an infrared thermometer (Raynger® ST™).

During the first measurement period, all individuals of both species exhibiting the 'standing' posture were noted, and temperature measurements taken. Temperature readings were also taken for a similar number of individuals in the normal 'flat' posture in crevices or under shaded overhangs (see Fig. 4A, B).

Over the first two days 12–15 individuals for each species were sampled, but on the third and fourth days, there were respectively only two and three individuals of 'standing' *A. unifas-*

ciata, and also fewer 'standing' *N. pyramidalis*. Some *N. pyramidalis* were however in a 'lifted' position — one in which the opercular opening is closed, and though the shell is slightly lifted off the rock surface it is not in an obvious vertical/upright position (Fig. 5). However it is important to point out that (a) 'standing' posture was only observed in littorinids on exposed rock surfaces; (b) some individuals that were initially observed in the 'flat' posture subsequently adopted the 'standing' posture as the surface temperature of the rocks increased.

A General Linear Model (GLM) procedure on MINITAB (2003) was used to analyse the response variable, difference in temperature between the rock and shell temperatures ('TempDiff') with 'Species' and 'Posture' as the factors. When the interaction term, 'Species'x 'Posture' was not significant, the main factors were analysed using One-way ANOVAs. Only data for the first two days were used in this analysis as the sample sizes of 'standing' *A. unifasciata* individuals were too small for the third and fourth days. The variable, 'TempDiff' was regressed against 'Rock temperature' for the two postures, 'standing' and 'flat' in each species using MINITAB (2003). An analysis of covariance (ANCOVA) was performed using GLM (MINITAB 2003) with 'TempDiff' as the response variable, 'Posture' as the factor, and 'Rock temperature' as the covariate. This ANCOVA was applied to test for difference in slopes of the regressed lines between postures in each species. If the slopes were not found to be significantly different, a test of intercepts was undertaken; no test of intercepts would be carried out when slopes were significantly different.

Data for *N. pyramidalis* for the third and fourth day were analysed separately using One-way ANOVA with 'TempDiff' being the response variable and posture ('flat', 'standing' and 'lifted') as the factor, followed by Tukey's Test for multiple comparisons when the test results were significant. The behaviour of the littorinids in rock pools was also noted during the field work.

RESULTS

The time at which the lowest tide occurred influenced the temperature profiles of the rocks (Fig. 1). On 19 and 20 February, the temperatures
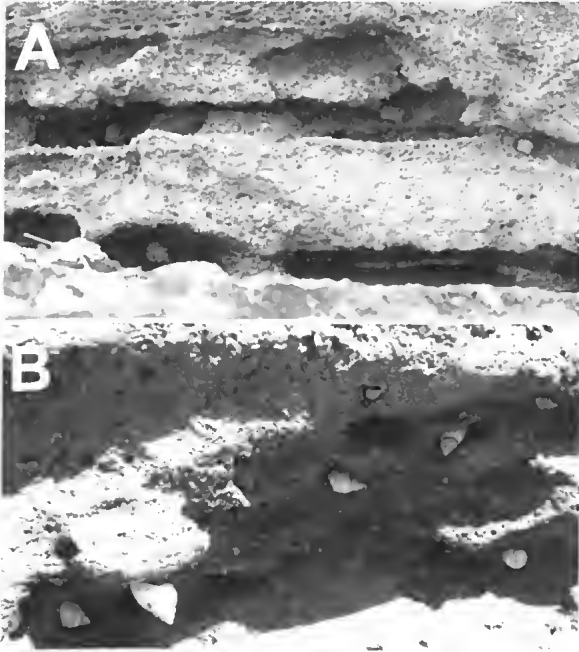
FIG. 5. *Nodilittorina pyramidalis* in the 'lifted' position.

FIG. 4. Crevices and overhangs in rock boulders with sequestered individuals of: **A**, *Nodilittorina pyramidalis*; **B**, *Austrolittorina unifasciata*.

of the rocks at lowest tide (i.e., at the intersection of the regression line and the time of lowest tide) were less than 35°C. In contrast, surface temperatures of rocks on 21 and 22 February were above 35°C (Fig. 1), with maximum temperatures of the rocks exceeding 40°C. On the days when substrate surface temperatures were in excess of 35°C, no *A. unifasciata* individuals were in the 'standing' posture. These littorinids were generally not as active throughout the six hours of observation in these two days compared with the first two days of the study. It was observed that some *N. pyramidalis* individuals did not completely assume the 'standing' posture; their apertural openings were sealed with the operculum and the shells were lifted slightly off the rock surface.

Observations of littorinids' behaviour on the rock surfaces and in small tide pools as ambient temperature rose revealed some interesting behaviours. Individuals of *N. pyramidalis* that remained in the tide pools after the tide had receded (Fig. 6A) began leaving the 'hot water bath' to climb up the sides of the tide pool (Fig. 6B). Once out of the tide pools, the littorinids

withdrew their foot, and then closed their apertural opening (Fig. 6C) before adopting the upright 'standing' posture on the rim of the apertural opening (Fig. 6D).

There was no significant interaction between the factors, 'species' and 'posture' (p>0.05, Table 1) for the first two days' data. Subsequent One-way ANOVA tests showed that temperature difference was only significantly different for 'posture' (TempDiff$_{flat}$ < TempDiff$_{standing}$) but not for 'species' (Table 1). Mean TempDiff for 'flat' and 'standing' postures, regardless of species, were 0.10 ± 0.61°C (n = 125) and 0.71 ± 0.89°C (n = 91) respectively. Analyses of covariance (ANCOVA) showed that there was no significant difference (p>0.05) between the slopes and intercepts of the regression lines of Temp-

Table 1. Results of Two-way ANOVA of the response variable, 'Temperature difference' (i.e., Rock temperature–Shell temperature) for the factors, 'Species' (i.e., *Nodilittorina pyramidalis* and *Austrolittorina unifasciata*) and 'Posture' (i.e. 'standing' and 'flat').

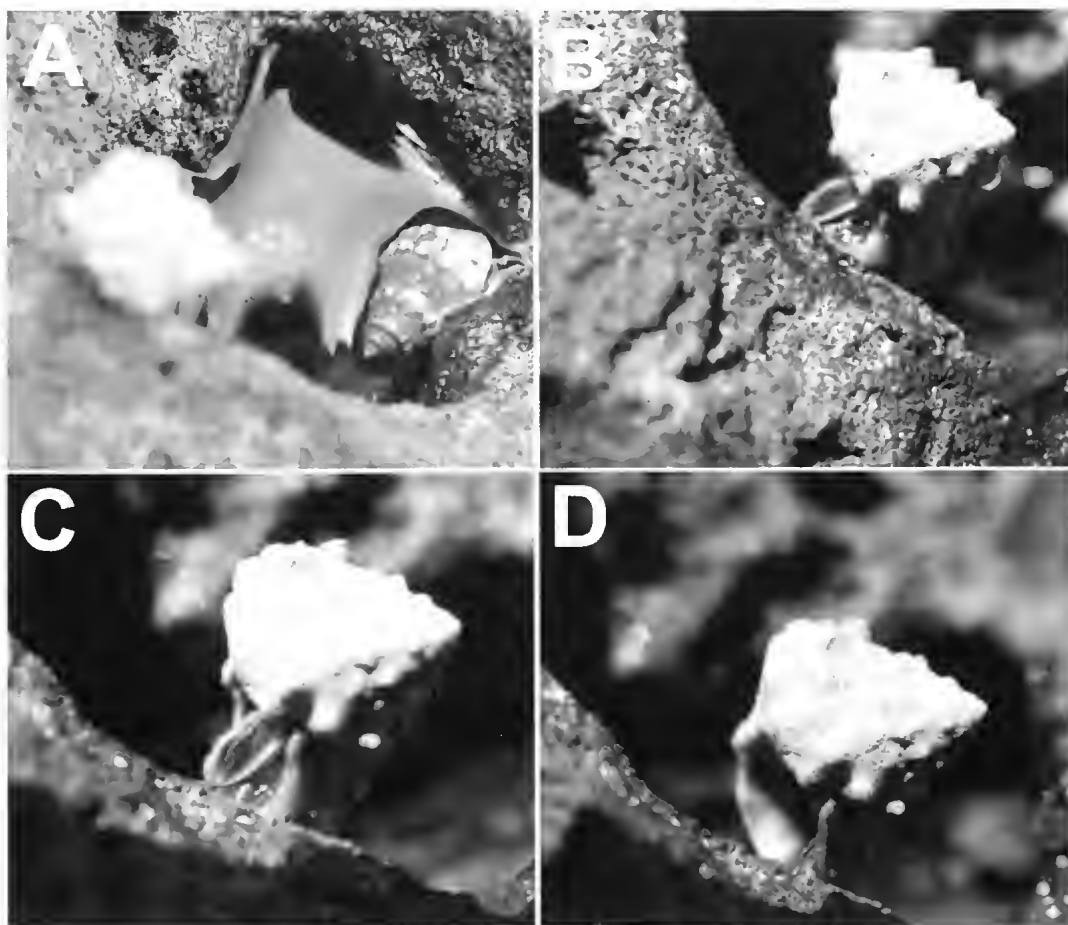|	Source of variation	F	df$_1$, df$_2$	p	
Full Model	Species	1.56	1, 212	0.214	
	Posture	32.85	1, 212	0.000	
	Species x posture	0.00	1, 212	0.978	n.s.
Main Factors	Species	1.59	1, 213	0.208	n.s.
	Posture	33.07	1, 213	0.000	

FIG. 6. **A**, two *Nodilittorina pyramidalis* individuals in a small tide pool; **B**, the larger of the two crawled up the side of the rock pool; **C**, gradual withdrawal of the foot; **D**, closed apertural opening and upright 'standing' posture attained.

Diff against rock temperature (Fig. 2A & B) for 'standing' and 'flat' postures in both species (Table 2).

Results of the One-way ANOVA for the *Nodilittorina pyramidalis* data for the third and fourth days showed that there was a significant difference in TempDiff for the three postures ($F_{2,130}$ = 33.80, p = 0.000). Tukey's test showed that TempDiff$_{standing}$ was significantly greater than both TempDiff$_{flat}$ and TempDiff$_{lifted}$ but there was no significant difference between the latter two TempDiffs (i.e., TempDiff$_{lifted}$ ≈ TempDiff$_{flat}$ < TempDiff$_{standing}$). Mean TempDiff for 'lifted', 'flat' and 'standing' postures for *N. pyramidalis* for the third and fourth days were –0.02 ± 0.67°C (n = 29), 0.02 ± 0.52°C (n = 75) and 1.07 ± 0.73°C (n = 29) respectively.

DISCUSSION

Austrolittorina unifasciata rarely displayed 'standing' posture when rock surface temperature exceeded 35°C. On days when the low tide period occurred earlier in the day rock-surface temperatures were relatively lower (< 35°C) (Fig. 1). It appears that the rate at which the temperature of the rocks rises is the key to whether they assume a 'standing' posture or sequester themselves in crevices. The threshold temperature for the onset of this response seems to be about 35°C — snails can still move around on their foot to seek crevices or gradually attain the 'standing' posture at this temperature. When the whole foot is in contact with the substratum, there is heat input by conduction as well as insolation. McQuaid & Scherman (1988) reported that body temper-

Table 2. Results of ANCOVAs for the test of slopes and intercepts of regression equations of: *Nodilittorina pyramidalis*, 'Standing' versus 'Flat'; *Austrolittorina. unifasciata*, 'Standing' versus 'Flat'. n.s. = not significant.

	Predictor	p	
Noditittorina pyramidatis	Posture	0.886	n.s.: Intercepts not different
	Rock temperature	0.435	
	Posture x Rock temperature	0.787	n.s.: Slopes not different
Austrotittorina unifasciata	Posture	0.391	n.s.: Intercepts not different
	Rock temperature	0.087	
	Posture x Rock temperature	0.178	n.s.: Slopes not different

atures of the paler *Littorina africana africana* using foot attachment to the substratum, were similar to those of *L. africana kynsnaensis*, a darker-shelled species, and this suggests that conductive heat gain may be just as important as insolation.

On the third and fourth days of the study, the snails were exposed later in the day when the ambient temperature was much hotter. As a result, rock temperatures rapidly rose past the crucial 35°C temperature. Very few of snails had the opportunity to assume the 'standing' posture before it became too hot. The 'lifted' posture could be the arrested/interrupted stage in the process of 'standing' in instances when heat stress becomes so extreme that it has to abort any attempt to become upright and close its operculum completely. This aspect of the heat response of these two species needs further investigation. It is also pertinent to note that during the first two days of the study, quite a lot of movement of snails was observed after the rocks were exposed. In contrast, there was hardly any snail that crawled on the rocks during the third and fourth day of the study. Further work is required to investigate the critical temperature at which the littorinids' foot is extended.

In Vermeij's (1973) discussion of dissipation of absorbed thermal energy by re-radiation and convection in littorinids, he emphasised the importance of a large shell surface area. He postulated that the increased surface area of nodulose shells means they are better radiators of absorbed thermal energy. Results of the present ANOVA showed that regardless of species, only the posture of snails significantly affected 'TempDiff', suggesting that even in pits or crevices, the nodulose *N.*

pyramidalis and the smooth-shelled *A. unifasciata* are similarly heated. This finding contrasts with both Vermeij's (1973) prediction and with Britton's (1995) report that both nodules and posture of *L. striata* aided to relieve thermal stress by re-radiation and convection. Lee (2003) reported similar TempDiff in individuals of the nodulose *Echinolittorina malaccana* (previously known as *Nodilittorina trochoides*) with intact shells and filed-shells (i.e., with nodules removed), thereby providing evidence that an increase in surface area due to shell ornamentation might not be responsible for heat dissipation. Radiation that falls on a body may be absorbed, reflected or transmitted (Jones 2000), hence, the more heat energy that is reflected, the less is absorbed and transmitted. Rough, nodulated shells reflect more heat (Nybakken 2001). Lee (2003) also observed that (1) the nodules of *E. malaccana* were of a much lighter colour than the rest of the shell and (2) filed-shells were darker in colour as compared with intact shells. She concluded that the shell ornamentation enhanced heat reflection. From the added evidence provided by this study, I suggest that when littorinids are sequestered in pits and crevices, nodules do not facilitate heat stress reduction as reflection is minimal in the shade.

The present results showed that *N. pyramidalis* individuals in the 'lifted' posture were not any cooler than those in the pits or crevices, indicating that perhaps the 'standing' posture offers the optimum heat reduction. McQuaid & Scherman (1988) reported that pits not only provide some shade from the sun but also offer

a substratum which may be 3–4°C cooler, resulting in lower body temperatures in *Littorina africana africana* and *L. africana knysnaensis*. 'Standing' posture, was, however, not reported in their paper to provide a comparison with present study. Lang *et al.* (1998) also reported that body temperatures of crevice occupants were cooler than those of individuals found on exposed areas in four Jamaican littorinids. Mineralogy of the substratum may account for large variations of the micro-environment (Britton *et al.* 1991). Although results of the ANCOVA test showed that the rate of change in the 'TempDiff' in response to rising rock temperature was similar for the two postures in both species of littorinids, it can be seen that 'TempDiff' for 'standing' snails was consistently higher than that of snails in the 'flat' posture in both species. This further substantiates the advantage of using the 'standing' posture as a strategy to overcome heat stress. The fact that *N. pyramidalis* crawls out of rock pools to assume the 'standing' posture (Fig. 6A–D) further reinforces that this is a better strategy than remaining in a 'hot water bath' that while it may prevent desiccation, must still reach an intolerable temperature.

Other behavioural adaptations have been suggested to help thermal regulation in high shore gastropods. Garrity (1984) noted that *Littorina aspera* and *L. modesta* used both holdfasts and orientation of the shell spire to minimise solar energy absorption. In contrast, no discernible pattern in the shell orientation was observed in seven species of Jamaican littorinid gastropods (Lang *et al.* 1998), and similarly *Littorina africana africana* and *L. a. knysnaensis* did not show any significant tendency for shell orientation (McQuaid & Schermann 1988). These contrasting observations suggest that behavioural adaptation may vary with local conditions, or with differences in the microenvironment, or may be species-specific. Shell spire-orientation in littorinid populations exhibiting 'standing' posture merits further study to determine whether the species involved is a thermal conformer or thermal regulator.

The present study showed that a 'standing' posture appears the most effective strategy for alleviating heat stress, but may be part of a complex response to various interacting factors

such as differences between individual species, substratum characteristics, length and timing of tidal exposure, and regional climatic regimes. Further studies will be necessary to better determine the factors that elicit the 'standing' posture.

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The use of infrared spectroscopy as a test for species-specific pedal mucus in gastropod molluscs — a comparative study in Moreton Bay and Singapore

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ABSTRACT

Infrared (IR) spectroscopy was used to study pedal mucous characteristics of eight species of marine gastropods to determine if it was useful for species identification. Three species of *Nerita*, two morphologically indistinguishable species of *Littoraria* (*L. articulata* and *L. strigata*) and one species each of *Nodilittorina*, *Austrolittorina* and *Echinolittorina*, were compared with a terrestrial snail, *Achatina fulica*. The IR spectra all showed high absorption in the 900–2100 cm^{-1} wave number region. No benzene overtones were observed at low wave numbers (1800–2000 cm^{-1}) suggesting that aromatic amino acids could be lacking in core glycoprotein molecules. Strong absorption bands at peaks of 1644 cm^{-1} and 1545 cm^{-1} were obtained for all species and attributable to amide-I and amide-II peaks respectively. Amide I (range 1600–1720 cm^{-1}) to Amide II (1500–1600 cm^{-1}) band area ratios ranged significantly: *Nerita* species: 1: 0.10–1: 0.22; *Achatina fulica* 1: 0.40; and *Littoraria* sp. 1: 0.48; *Austrolittorina unifastciata*: 1: 0.57; *Echinolittorina malaccana*: 1: 0.65 and *Nodilittorina pyramidalis*: 1: 0.74. These differences appear useful for distinguishing between the six genera and congeneric species studied. ❑ *infrared, intertidal, snail, spectroscopy, Singapore, marine, Moreton Bay, mucus, Queensland.*

Molluscan mucus is made up of many compounds such as lectins, charged muco-polysaccharides, glycoproteins, proteins, uronic acid, sialic acid hexosamine and a host of other molecules in an aqeous medium (Schlichter 1982; Cottrell *et al.* 1993, 1994; Furuta *et al.* 1995; Davies & Hawkins 1998). It is generally used for the protection of cell surfaces exposed to the external environment (Davies & Hawkins 1998). Information about the mollusc's sexual state and direction of locomotion is also conveyed to conspecifics and predators by the mucus (Denny 1989). The mud snail, *Ilynassa obsoleta*, (Say, 1822) follows polarised trails of conspecifics in the pursuit of mates, but ignores non-conspecific trails (Bretz & Dimock 1983). Similarly, Erlandsson & Kostylev (1995) reported that male *Littorina littorea* track females using cues from conspecific trails, but ignore the trails of other males. Thus, both species-specific and gender specific cues are known to occur within gastropod mucus.

Cottrell *et al.* (1993) used SDS-PAGE electrophoresis of mucus to distinguish between seven snail species, however, such analysis requires complicated preparation and purification of the sample. Recently, infrared (IR) spectroscopy has been proposed as a simple method to study molluscan mucus (White *et al.* 1997; Skingsley *et al.* 2000), as lengthy sample preparation is unnecessary and results of spectra analyses can be obtained within seconds. Skingsley *et al.* (2000) successfully used IR spectroscopy of mucus to distinguish between six species of slugs, using two species of terrestrial snails, *Helix aspersa* and *Cepaea nemoralis* for comparison.

The identification of many mollusc species is difficult, and often requires dissection to study subtle differences in internal organ structure. Reid (1986) reported that it was difficult to distinguish between *Littoraria strigata* and *L. articulata* merely by their shells, and additional examination of anatomical features (e.g. penial form) was required. Lee (2003) when conducting a field study on the distribution, modes of attachment, and heat tolerance of Singapore littorinids, had to lump together *Littoraria articulata* and *Littoraria strigata* under *Littoraria* sp., as the shells of these two species are too similar in colour and morphology to be able to separate in the field. The objective of the present study was to test IR spectroscopy of pedal mucus for its efficacy in distinguishing between eight species in the genera, *Austrolittorina*, *Echinolittorina*, *Nodilittorina*, *Nerita* and *Littoraria*.

MATERIALS AND METHODS

Five individuals of *Austrolittorina unifasciata* (Gray, 1826) (= *Nodilittorina unifasciata*, see Reid, 2007) and *Nodilittorina pyramidalis* (Quoy & Gaimard, 1833) were collected from the high intertidal rocky shore at Hospital Bay, Dunwich, North Stradbroke Island on 23 February 2005, and kept in moist containers for transport back to the laboratory in Singapore. Similarly several individuals of *Echinolittorina malaccana* (Gray, 1839) (= *Nodilittorina trochoides*, see Reid, 2007), *Nerita lineata* Gmelin, 1791, *Nerita planospira* Anton, 1839, *Nerita chamaeleon* Linnaeus, 1758, and *Littoraria* sp. were also taken from the Pasir Ris Nature Area in Singapore. Five individuals of the giant African snail, *Achatina fulica* Bowdich, 1822 were collected from Singapore. The spectrum obtained from the pedal mucus of this terrestrial pulmonate was used to compare with the marine gastropods' spectra. Specimens were used within five days of collection. Marine gastropods were wetted with artificial seawater to induce them to crawl, while tap water was used for the giant African snail. Snails may produce a defense mucus that could have properties different from normal body mucous secretions, and therefore the snails were handled several times in order to habituate them. As long as the stimulus is non-threatening, habituation is rapid (Carew & Sahley 1986).

The entire foot of each snail was swiped across a barium fluoride crystal IR window, thereby coating it with a thin layer of mucus. This mucus was analysed 'raw' which reduces the chance of artifact from any derivative procedure. Infrared spectroscopy in transmission mode was used, i.e., a spectroscopic beam was passed through the sample and crystal. The mucus was too viscous for injection into a normal transmission cell. The presence of liquid water, water vapour and barium fluoride bands disrupt the spectral profile, and therefore these were subtracted off-line from the raw mucus specimen. The corrected spectra were assigned bands that equate to the likely chemical components of the mucus using standard banding protocols developed by Williams & Fleming (1987). The IR spectra were recorded at a resolution of 2 cm^{-1} in the spectral range of 900–2000 cm^{-1} using a Perkin-Elmer Fourier transform infrared spectrometer. The sampling procedure was repeated five times for each species, and several individuals were used to reduce the likelihood of biological variability affecting the results.

RESULTS

The IR spectra of all gastropods show high absorption in the 900–2000 cm^{-1} wave number region, and this region contains particularly significant information on the organic components of the mucus (see Williams & Fleming 1987). In all species studied, there were strong absorption bands at peaks of 1644 cm^{-1} and 1545 cm^{-1}. These bands show the presence of amide bonds in the core proteins of both glycosaminoglycans (GAGS) and proteoglycan molecules, including lectins (Davies & Hawkins 1998), and are attributable to amide-I and amide-II peaks respectively. The shape of the amide bands, and the size of the area under them, provide useful information on the presence of β-sheets and β-turns (Surewicz *et al.* 1993).

The broad absorption band around the 1400 cm^{-1} region indicates the presence of different ionisation states of the carboxylate groups associated with acid derivatives of sugars and some amino acid side chains ($COOH \leftrightarrow COO^- + H^+$). Generally, CH_2 vibration occurs at 1450 cm^{-1} and CH_3 vibration at 1380 cm^{-1} and bands are due to the presence of the core carbon spines of
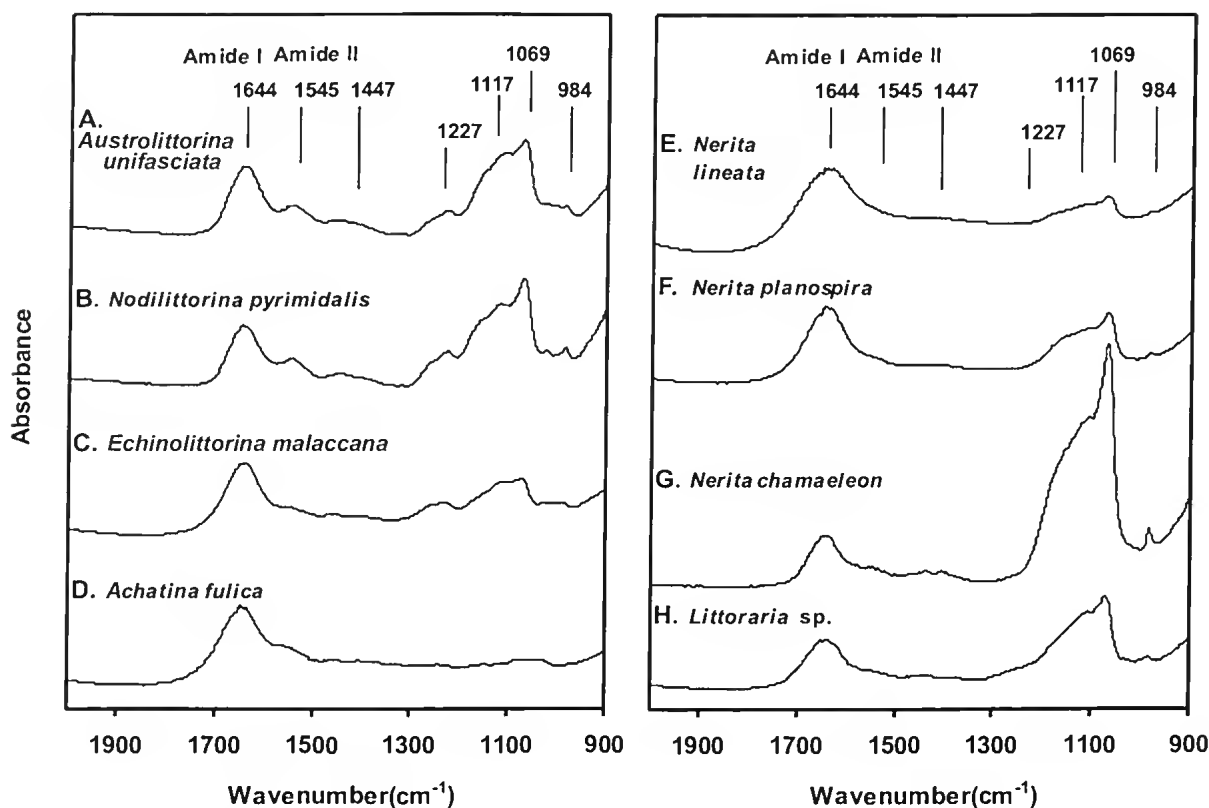
FIG. 1. Infrared spectra of the pedal mucus from: **A**, *Austrolittorina unifasciata*; **B**, *Nodilittorina pyramidalis*; **C**, *Echinolittorina malaccana*; **D**, *Achatina fulica*; **E**, *Nerita lineata*; **F**, *Nerita planospira*; **G**, *Nerita chamaeleon*; **H**, *Littoraria* species.

proteins, carbohydrates, and possibly lipids. A series of IR absorption peaks in the 950–1300 cm⁻¹ region show the presence of a large quantity of OH and O-glycosidic bondings, as well as the occurrence of sulphated, acylated, and esterised compounds — all species in this study showed these peaks.

The typical IR spectra of *Austrolittorina unifasciata*, *N. pyramidalis* and *E. malaccana* mucus are shown in Fig. 1A–C. The measurements of band areas of Amide I and Amide II peaks at 1644 cm⁻¹ and 1545 cm⁻¹ respectively were obtained using software included in the Perkin-Elmer spectrometer system. These peaks indicate that protein amides with β-sheeting and β-turns are present in all three species. Table 1 shows the band area ratios of Amide I (1600–1720 cm⁻¹) to Amide II (1500–1600 cm⁻¹) for these three littorinid species. The band area ratios were determined with an accuracy of 0.01. The differences in these

ratios reflect relative amounts of molecular ionisation and hydration. The band area ratio of *E. malaccana* (from Singapore) lies between that of the two Australian littorinid species.

Figure 1D shows the IR spectrum of the terrestrial snail, *Achatina fulica*. Absorption peaks at 1644 cm⁻¹ and 1545 cm⁻¹ indicate the presence of Amide I and Amide II respectively, but the band area ratio of 1:0.40 is smaller than that of all three littorinid species, and appears to reflect significant generic and specific level separation (Table 1).

The IR spectra of *Nerita lineata*, *N. planospira*, and *N. chamaeleon* show a strong Amide I peak at 1644 cm⁻¹, but a very weak Amide II peak at 1545 cm⁻¹ (Fig. 1E–G), and consequently the band area ratios are much lower than those of all three littorinid species and of *Achatina fulica* (Table 1). Thus the relative amounts of molecular ionisation and hydration in the mucus of

Table 1. Band area ratios of Amide I (at 1644 cm⁻¹) to Amide II (at 1545 cm⁻¹) in infrared spectra of pedal mucous from species of *Austrolittorina*, *Nodilittorina*, *Echinolittorina*, *Achatina*, *Nerita* and *Littoraria*.

Genus	Species	Locality	Band area ratios
Austrolittorina	*A. unifasciata*	Moreton Bay, Australia	1:0.57
Nodilittorina	*N. pyramidalis*	Moreton Bay, Australia	1:0.74
Echinolittorina	*E. malaccana*	Pasir Ris Nature Area, Singapore	1:0.65
Achatina	*A. fulica*	National Institute of Education, Singapore	1:0.40
Nerita	*N. lineata*	Pasir Ris Nature Area, Singapore	1:0.10
	N. planospira	Pasir Ris Nature Area, Singapore	1:0.15
	N. chamaeleon	Pasir Ris Nature Area, Singapore	1:0.22
Littoraria	*L. articulata* +*L. strigata*	Pasir Ris Nature Area, Singapore	1:0.48

the *Nerita* species are significantly different from those of the other species in this study. The band area ratio for the samples of the cryptic *Littorina* species-pair (*L. articulata* and *L. strigata*) was 1:0.48. This value was quite consistent between individuals and no significant differences were detected that might help reflect species differences. The band area ratio for *Nerita* is intermediate between that of the terrestrial genus *Achatina* (*A. fulica*) and those of the intertidal littorinid species in this study (Table 1).

DISCUSSION

The different Amide band ratios indicate that protein cores of the mucus of the individual species are different although all showed the presence of β-sheet and β-turn structural elements. The Amide band area ratios formed distinct groupings consistent with the six genera studied (Table 1) and thus may have generic significance although a greater range of species within each genus will need to be analysed before this can be conclusively stated. Different values for band area ratios were obtained for each species (Table 1), hence there is potential for reliable congeneric specific separation. With an experimental accuracy of 0.01, the band area ratio values (Table 1) are distinct for each species, i.e., the ratio values do not overlap and species-specific differentiation is possible.

In contrast, Skingsley *et al.* (2000) reported that there was little difference in the band area ratios for all the gastropods in their study, and only provided the ratio for *Arion ater* var. *rufus*

(Linnaeus, 1758), i.e., 1: 0.68. This ratio of 1: 0.68, though close to *E. malaccana*'s 1: 0.65 and *N. pyramidalis*' 1: 0.74 values, is distinct from all ratio values reported in the present study. This suggests the possibility of species differentiation using band area ratios. Unfortunately individual band area ratios for the other species studied by Skingsley *et al.* (2000), i.e., *Arion subfuscus* (Draparnaud, 1805), *Arion hortensis* Férussac, 1819, *Deroceras reticulatum* (Muller, 1774), *Deroceras carnanae* (Pollonera, 1891), *Limax maculatus* (Kaleniczenko, 1851), *Helix aspersa* Muller, 1774, and *Cepaea nemoralis* Linnaeus, 1758, were not reported. More IR spectroscopy analyses of the mucus of other mollusc genera are needed.

Similar absorption peaks in the 900–1450 cm⁻¹ wave number region were observed for all three rough periwinkle species as shown in the IR spectra (Fig. 1A–C). The 1447 and 1227 cm⁻¹ peaks indicate the presence of carbon spin of the core proteins in the form of CH_2 and CH_3 relating to the composition and ionisation state of the amino acid side chains and sugar side chains (e.g., COOH, COO⁻). In this spectral region, the absorption peaks at 984, 1069, 1117 cm⁻¹, and some weaker peaks which overlap with the broad bands around 1450 cm⁻¹ region are all indicative of sulphated, acylated and esterified molecular structures in the mucus. In this regard our three littorinid species are very similar to the aquatic species *Lymnaea stagnalis* (Linnaeus, 1758), studied by Skingsley *et al.* (2000), and all differ from the terrestrial species *Arion subfuscus*, *Helix aspersa*, and *Arion ater* var. *rufus*

studied by Skingsley *et al.* (2000), because of the absence of a 1385 cm⁻¹ peak in the IR spectra that is present in those species.

The IR spectra of all three *Nerita* species show similar features in the 900–1450 cm⁻¹ region (Fig. 1E–G). Peaks at 984, 1069 and 1117 cm⁻¹ were clearly observed. However, in this region, the spectra of the *Nerita* species lack the 1227 cm⁻¹ peak present in the three littorinid genera. This IR peak can probably be used to differentiate the two genera. Furthermore, the IR features in the 900–1450 cm⁻¹ region for the marine *Nerita* species (Fig. 1E–G) differ significantly from that of the terrestial *Achatina fulica* (Fig. 1D).

The IR spectrum of *Achatina fulica* shows the peaks in the 900–1450 cm⁻¹ region are much weaker and different from those in the three species of the genus, *Nerita* as well as from that of the other three genera, *Austrolittorina*, *Echinolittorina* and *Nodilittorina* (Fig. 1D). The weak absorption peaks at 1033, 1070, and 1150 cm⁻¹ for *Achatina fulica* were absent in the spectra of the three littorinid species. The differences in the IR features clearly indicate differences in the composition and ionisation state of the amino acid side chains and sugar side chains (e.g., COOH, COO⁻), as well in the level of sulphated, acylated and esterified structures in the species. These differences are sufficient to set the pulmonate *Achatina fulica* apart from all the intertidal species in the present study.

Cottrell *et al.* (1993) reported that the aromatic amino acids in the core of glycoprotein molecules are represented by benzene ring overtones in the low wave number region from 1800–2000 cm⁻¹. In our present study, benzene ring overtones were not observed in the IR spectra of any of the species (Fig. 1A–H). This could indicate that benzene-containing amino acids such as phenylalanine and tyrosine are absent in all of the species in this study. Distinct benzene ring overtones were only seen in three of the six terrestrial slugs, in only one of the two terrestrial gastropods, and totally absent in the aquatic gastropod studied by Skingsley *et al.* (2000). Thus, there is no consistent association between the presence or absence of benzene ring overtones with species, genera or habitat modes of gastropods.

The IR spectra of solids and liquids, in the present study, are expected to show broad absorption bands which tend to overlap. However, the overlapping may not seriously affect the peak positions. It may provide a spectral morphology which is unique to each species. However, due to presence of water inherent in the mucus, spectral features may be altered significantly. Therefore, it is not reliable to use spectral morphology as a tool to differentiate species.

We conclude that it is premature to advocate that IR spectroscopy could be used as a tool for species identification as suggested by Skingsley *et al.* (2000) owing to the many inconsistencies present in all the species studied to-date. However, from our results, it appears that band area ratios of the amine peaks may represent a potentially useful tool in distinguishing species.

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Relationships between groundwater composition and stimulation of the cyanobacterium *Lyngbya majuscula*

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ABSTRACT

The Pumicestone Passage/Deception Bay region of southeast Queensland, Australia, has experienced increased frequency and severity of blooms of the toxic benthic cyanobacterium *Lyngbya majuscula*. It is hypothesised that blooms are the result of landuse changes in the surrounding catchments leading to increased nutrient and organic matter loads to waterways. Previous studies investigating the response of *L. majuscula* to diluted groundwaters from across Deception Bay/Pumicestone Passage showed groundwater from acid sulfate soils, exotic pine plantations and *Melaleuca* vegetation significantly stimulated *L. majuscula* photosynthetic response in laboratory bioassays. The results of the previous study are expanded by investigating the composition of these 74 groundwaters to ascertain what factors contribute to the observed differences in *L. majuscula* response. A multiple regression analysis showed the total iron, pH, conductivity, total phosphorus and dissolved organic carbon contents in groundwater accounted for 58% of the variation in *L. majuscula* response. Total iron content of the groundwater had the highest correlation accounting for 28% of the variation in response. Other significant correlations included ammonium nitrogen, total phosphorus and electrical conductivity. Significant responses to iron, phosphorus and nitrogen concentrations in experiments involving addition of pure chemicals has previously been found for both laboratory based bioassays and *in situ* field experiments. The response to electrical conductivity is probably the result of a correlation with acid sulfate soils whose groundwater has been shown to significantly stimulate *L. majuscula* response. As landholders commonly identify and manage land through vegetation, soils, geology and landuse, these categories were used to statistically assess groundwaters. Based on the groundwater relationships, land with *Melaleuca*, pine or *Casuarina* vegetation, or with Hydrosols, Podosols or acid sulfate soils present, or formed from marine sediments, needs to be carefully managed to limit nutrient export that could boost *L. majuscula* growth Our conclusions can be used to confirm or adjust hazard ratings in the Nutrient Hazard Model. ❑ *cyanobacteria, groundwater, growth, landuse, Lyngbya majuscula, Moreton Bay, nutrients.*

Harmful algal blooms are becoming more numerous, widespread and persistent in nutrient-enriched tropical and subtropical marine ecosystems (Paerl 1988). One species of concern is the benthic filamentous, non-heterocystous nitrogen-fixing cyanobacterium *Lyngbya majuscula* which in recent years, has bloomed in eutrophic estuaries, embayments and reef environments across the world (Diaz *et al.* 1990; Albert *et al.* 2005). Blooms have had adverse environmental and economic impacts, including directly overgrowing and smothering intertidal and subtidal benthic communities such as seagrass and coral (Stielow & Ballantine 2003). Additionally, *L. majuscula* contains secondary metabolites and toxins (reviewed in Osborne *et al.* (2001)), which have caused asthma, dermatitis and eye irritation in humans, and have been linked with increased tumour occurrence in marine turtles (Arthur *et al.* 2006).

Increased frequency and severity of freshwater and marine blooms of *Lyngbya* species in several different systems worldwide (Diaz *et al.* 1990; Speziale & Dyck 1992; Dennison *et al.* 1999), has been linked to anthropogenic nutrients, supplied through terrestrial runoff and groundwater. Similarly, blooms of *L. majuscula* in northern Deception Bay, southeast Queensland, Australia, have been linked to landuse changes resulting in increased loads of nutrients and dissolved organic matter in the creeks and water-bodies adjacent to the bloom site, especially after significant rainfall events (Ahern *et al.* 2007b; Dennison *et al.* 1999; Albert *et al.* 2005). In an effort to reduce the intensity and severity of blooms, local and state regulatory authorities expressed a desire to identify areas and landuse activities most likely to supply/transport bioavailable nutrients and organic matter to bloom sites to allow management to focus on the higher-hazard areas. However, the amount and form of nutrients/organic matter in runoff, or transported in groundwaters from a particular parcel of land, is influenced by complex interactions involving geology, soils, vegetation, present and past landuse, and human activities (Pointon *et al.* 2004). While nutrient analyses of the soils and groundwater from different areas within the catchment are important, biological information on *L. majuscula* growth is necessary to effectively interpret such data.

Laboratory-based biological assays have been employed to test *L. majuscula* growth responses to soils, leachates and groundwaters from different areas across the Pumicestone Passage/Deception Bay catchments (Ahern *et al.* 2003, 2006a; Albert *et al.* 2005). Preliminary bioassays showed that the addition of diluted soil extracts (Albert *et al.* 2005) and groundwaters (Ahern *et al.* 2003) from exotic pine plantations and *Melaleuca* communities on acid sulfate soils (ASS) stimulated *L. majuscula* productivity. Using this information, combined with Geographic Information System (GIS) coverages, published information, and limited laboratory analyses of soils and groundwaters, the first version of a 'Nutrient Hazard Model' (termed 'Hazard Model' for the remainder of the paper) was developed to predict areas vulnerable to the export of nutrients (Pointon *et al.* 2004). Since then, the model has gone through an iterative process of revisions as new data or findings become available with map outputs from the revisions of the earlier Hazard Model being used to support *Algal Blooms* policy 2.4.7 within the *Southeast Queensland Regional Coastal Management Plan* (EPA 2006). To further improve the Hazard Model, a more comprehensive bioassay study of 74 groundwaters representing 10 major landuse/vegetation/soil systems from across the Deception Bay/Pumicestone Passage catchments was conducted. This showed groundwater from areas of ASS, exotic pine plantations and *Melaleuca* vegetation (paperbark swamps) significantly stimulated *L. majuscula* photosynthesis (Ahern *et al.* 2006a).

OBJECTIVES

This study expands on the detailed bioassay work of Ahern *et al.* (2006a) by investigating the physico-chemical and nutrient composition of the 74 groundwaters to ascertain the main factors contributing to the observed differences in *L. majuscula* photosynthetic response. Relationships between *L. majuscula* response and groundwater properties/nutrients are explored using a range of statistics, in order to confirm and/or improve predictive ability of the latest version of the Hazard Model (Pointon *et al.* 2008).

As landholders commonly identify and manage land by features such as vegetation, soils, geology and landuse, these themes, with the

addition of ASS and geology have been used to statistically assess groundwaters. This will support the identification of areas requiring greater management attention and higher hazard ratings in the Hazard Model.

METHODS

STUDY AREA

Sampling was conducted in the catchments of rivers and steams that flow into Deception Bay and Pumicestone Passage, Southeast Queensland, Australia (Fig. 1). These catchments have been extensively impacted by human development, including rapidly expanding urban and rural/residential areas adjacent to landuse changes such as: livestock grazing; the removal of natural vegetation; extensive *Pinus elliottii* plantation forestry; horticulture; agriculture; sand/gravel extraction; and, intensive poultry farming. These catchments adjoin the shallow tidal seagrass beds of northern Deception Bay that have been subject to summer blooms of *L. majuscula* (Fig. 1). Bribie Island, where there were numerous sites, is often simply referred to in the text as 'Bribie'.

SITE SELECTION AND SAMPLING

Shallow groundwater was collected from 74 sites representing 10 major landuse/vegetation/soil combinations (Table 1), chosen because of their large spatial area, close proximity to waterways, or the results from previous laboratory bioassays (Ahern *et al.* 2006a). At each site, piezometers wells (50 mm inside diameter and slotted at the required depth to allow groundwater inflow) were installed using a percussion-assisted drilling device (Geoprobe®, Salina, Kansas, USA) to auger a hole (~60 mm diameter) to a depth that intercepted the shallow (<3 m) water-table or shallow aquifer. In waterlogged areas (such as *Melaleuca* swamps on Bribie I.), the 'surface water' was also collected. Collection of water samples was not undertaken until at least 7 days after the well was installed to allow for settling. Prior to collecting the samples, the wells were purged using a submersible pump to remove 'older water' present and allow inflow of groundwater into the well.

Samples were collected by pumping groundwater directly from the well through an inline filter into clean (acid and deionised water washed) bottles. To minimise oxygen contamination, bott-

les were overfilled to ensure no air bubbles were present prior to capping. For dissolved nutrient and organic carbon analyses, sampled water was filtered through 0.45 μm membrane filters. Samples for dissolved metal analysis were also filtered and fixed with 5mL of 70% nitric acid (v/v). For ferrous (Fe^{2+}) iron concentrations, a measured aliquot of the 0.45 μm filtered groundwater was immediately added to pre-weighed ferrozine solution in tubes in the field before any oxidation could occur. Samples high in ferrous iron content (as indicated by intense purple colour) were repeated with a smaller aliquot. All water samples were immediately placed on ice and on return to the laboratory stored at <4° C in the dark until used in the bioassays (within 24 hours) or analysed for nutrients.

At the same time as piezometer installation, an undisturbed soil core (40 mm in diameter) was collected using Geoprobe® hollow barrels. Soil depth increments were sampled depending on the horizonation of the particular soil, but generally were 0–10, 20–30, 50–60, 80–90, 110–120, 140–150, 180–200, 230–250 and 280–300 cm. The soil cores were described according to the Australian Soil and Land Survey Field Handbook (McDonald *et al.* 1990) and classified as per The Australian Soil Classification system (Isbell 1996), Great Soil Group system (Stace *et al.* 1968) and A Factual Key for the Recognition of Australian Soils (Northcote 1984). Acid sulfate soils were identified by soil profile morphology, peroxide field pH tests (Ahern *et al.* 1998) and confirmed by laboratory analyses.

NUTRIENT ANALYSIS

Water samples were analysed for pH (4500H) and electrical conductivity (2510A). Soluble ammonium (NH_4-N) (4500NH3H), oxidised nitrogen (NO_x-N) (4500NO3-I) and orthophosphate (PO_4-P) (4500PG) were determined on a Foss STAR5000, Flow Injection Analysis Colorimeter (APHA/AWWA/WEF, 2005). Dissolved Kjeldahl nitrogen and phosphorus were also determined by Flow Injection Analysis Colorimetry after Kjeldahl digestion. Dissolved inorganic (5310A) and organic carbon (5310D) was determined using a Non-Dispersive Infra Red (NDIR) detection cell (APHA/AWWA/WEF, 2005). Dissolved metal contents were determined

FIG. 1. Map of Deception Bay/Pumicestone Passage catchments showing sampling locations of the 74 shallow groundwater sites.

Table 1. Description of the 10 landuse/vegetation/soil systems used in groundwater experiments of *L. majuscula* bioassays (adapted from Ahern *et al.* 2006b).

Group	ASS presence	Landuse/vegetation class	No. of sites
Melaleuca	ASS	Remnant native vegetation	12
	No	Remnant native vegetation	4
Casuarina	ASS	Remnant native vegetation	9
	No	Remnant native vegetation	6
Disturbed' and/or cleared landscapes	ASS	Urban, canal development, sand extraction, horticulture	10
	No	Urban, horticulture, grazing	6
Pine on mainland Pine on Bribie Is	No	Plantation forestry (younger, older and cleared plantations)	9 6
Eucalypt	No	Remnant native vegetation	7
Wallum heathland	No	Remnant native vegetation	5

using Inductively Coupled Plasma Optical Emission Spectrometry (ICPOES) (Varian Vista Pro and Thermo TJA IRIS) (APHA/AWWA/WEF, 2005). Ferrous iron concentrations were determined by the Ferrozine method (Stookey 1970) which involved reading the purple colour developed with Ferrozine reagent on a spectrophotometer (absorption peak at 562nm) and calibrating against standard solutions. For laboratory analysis of ASS, a selection of soil depths increments were analysed in the laboratory following the ASS methods of Ahern *et al.* (2004).

TESTING *LYNGBYA* RESPONSE TO GROUNDWATERS

L. majuscula photosynthetic response to each of the 74 groundwaters was ascertained by laboratory based biological assays using a ^{14}C-bicarbonate radioisotope technique documented in Ahern *et al.* (2006a).

DATA SYNTHESIS AND ANALYSIS

The program Statistica™ was used to perform all statistical analysis in the current study. To ensure assumptions of a linear model were met, visual diagnostics of the residuals were undertaken to check that the variances of the dependant variables were homogeneous and followed a normal distribution. If necessary, the variables were transformed by an appropriate power selected with a Boxcox test and the residuals rechecked for normality and variance homogeneity. When appropriate, Fisher's

least significant difference (LSD) was used to test for significant differences between means. Data on the nutrient concentrations (total iron, ferrous iron, total phosphorus, phosphate, total nitrogen, ammonium, NOx and DOC) and properties (conductivity and pH) of the groundwaters were correlated with *L. majuscula* response (i) individually and (ii) via multiple regression. Data used for the correlations and multiple regression were taken from all the 74 groundwater sites, except for extreme outliers, which were identified Mahalanobis distances. Additionally, data were organised and analysed according to various groupings including the 10 groups in Table 1, ASS status, vegetation type, general soil classification and broad geology.

MULTIPLE REGRESSION OF *LYNGBYA* RESPONSE VERSUS GROUNDWATER PROPERTIES

A multivariate stepwise regression was used to determine which groundwater properties/nutrients or combination of properties/nutrients best explained variation in *L. majuscula* productivity. Explanatory variables (groundwater properties/nutrients) used in the analysis were total iron, ferrous iron, total phosphorus, phosphate, total nitrogen, ammonium and NOx. Conductivity, pH and dissolved organic carbon (DOC) concentrations were also included as they can affect the chemical state, solubility and presumably influence the bioavailability of nitrogen, phosphorus and iron to *L. majuscula*.

A forward stepwise selection of parameters (total iron, ferrous iron, total phosphorus, phosphate, total nitrogen, ammonium, NOx, DOC, pH and conductivity) was performed using stepwise regression. The starting point was a model with no parameter effects (except intercept). Every possible parameter was included in the model in turn, and its effect was proved with Akaike's information criterion. At each step, the best explanatory (i.e., most informative) variable was selected. During the stepwise process, the effect of the elimination of previously selected parameters and the inclusion of a new one was valued, and the action that most improved the model was performed. This was continued until the most optimal model, comprising the best explanatory variables, was found. Finally, the significance of stepwise-model parameters was tested (using F statistics) and non-significant parameters ($P > 0.05$) were removed.

ANALYSIS OF GROUNDWATER DATA

Data from the different groundwaters were grouped and statistically analysed in five different ways according to: i) the 10 major landuse/soil/vegetation combinations (Table 1); ii) ASS status; iii) dominant vegetation; iv) soil order; and, v) the dominant geology/parent material. The purpose of this was to help isolate the main nutrients/groundwater properties contributing to differences in *L. majuscula* response between groups and secondly, to assist in the identification of areas in the Deception Bay/Pumicestone Passage area with high intrinsic potential to store and/or supply nutrients for *L. majuscula* growth. The later was deemed necessary to support the compilation and validation of the 'Hazard Model' compiled to identify areas vulnerable to supply and/or export of nutrients to *L. majuscula* blooms in southeast Queensland (Pointon *et al.* 2008).

For the 10 major landuse/soil/vegetation systems, a one-way ANOVA was conducted on each different nutrient and groundwater property. Similarly, separate one-way ANOVAs were conducted on vegetation (*Melaleuca, Casuarina*, wallum, eucalypt, pine and cleared/disturbed), soil order (Podosols, Hydrosols, Chromosols, Dermosols and Rudosols) and dominant geologies/parent materials (marine, alluvium and continental). Another one-way ANOVA was conducted on three vegetation types (*Melaleuca*, 'disturbed' and *Casuarina*) growing on ASS and non-ASS.

RESULTS AND DISCUSSION
LYNGBYA RESPONSE TO GROUNDWATER

The multiple regression of *L. majuscula* productivity with groundwater properties found that the dependant variables in order of significance were: total iron, pH, conductivity, total phosphorus and dissolved organic carbon (DOC), (the significance level, standardised Beta and B are shown in Table 2). The final model explained 58% of the variation in *L. majuscula* response ($R^2 = 0.58$; $F_{6,60} = 16.1$; $P < 0.0001$), and is expressed as:

Y = 0.12 total Fe + 0.76 pH + 0.11 conduct. + 0.16 total P − 0.11 DOC + 0.42

These five dependant variables along with a sixth, ammonium, which did not make a significant contribution to improving the R^2 of the regression, are discussed in detail below.

ROLE OF KEY NUTRIENTS

Nitrogen-fixing cyanobacteria, such as *L. majuscula* (Lundgren *et al.* 2003) are not necessarily dependant on an external source of nitrogen and instead phosphorus (essential for growth) and iron (required for photosynthesis and nitrogen fixation) often become limiting (Whitton & Potts 2000). The current study found concentrations of total iron, total phosphorus and ammonium in groundwater were individually significantly correlated with the photosynthetic response of *L. majuscula* in the bioassays (Table 3), as reported in Ahern *et al.* (2006a).

Iron. Iron is an essential micronutrient for the growth of all aquatic organisms and is particularly important for the nitrogen-fixation cyanobacterium such as *L. majuscula*, being an essential component in the nitrogenase enzyme (Paerl *et al.* 1987). Total iron in the groundwater had the highest (r = 0.53) and most significant ($P < 0.001$) correlation with *L. majuscula* photosynthetic response; with total iron accounting for 28% of the variation (Table 3). This agrees with previous laboratory studies (Gross & Martin 1996; Dennison *et al.* 1999; Ahern *et al.* 2006b), and with *in situ* field studies at two

Table 2. Multiple regression of *L. majuscula* relative productivity response to groundwaters vs various independent variables: $R^2 = 0.58$; $F_{6, 60} = 16.1$; $P < 0.0001$.

	Beta	B	P level
Intercept		0.42	$P = 0.39$
Total iron	0.503	0.12	$P < 0.0001$
pH	0.376	0.76	$P < 0.001$
Conductivity	0.353	0.11	$P < 0.001$
Total phosphorus	0.283	0.16	$P < 0.01$
DOC	−0.236	−0.11	$P < 0.05$

locations in Moreton Bay (the Eastern Banks (Ahern *et al.* 2007a) and Deception Bay (Ahern *et al* 2008) — where rapid growth of *L. majuscula* was observed following the addition of organically chelated iron to the water column.

As expected there was a highly significant ($P < 0.001$) correlation ($r = 0.61$) between ferrous and total iron, but while there was also a highly significant correlation between *L. majuscula* photosynthesis and total iron, the correlation with ferrous iron alone ($r = 0.13$) was not significant ($P > 0.05$). This is likely due to instability of the ferrous ion when added at a 1:19 ratio to slightly alkaline seawater (pH ~ 8.2), and open to the air for oxidation over the 5 days of the

bioassay. The soluble organically complexed iron in groundwaters (included in total iron measurement) was probably the main source for the *L. majuscula* photosynthetic response, especially because it can undergo photoreduction and release short-lived ferrous iron species into solution (Waite & Morel 1984) which *L. majuscula* is known to uptake directly (Rose *et al.* 2005).

Phosphorus. Phosphorus is essential for all metabolic processes and consequently has been commonly recorded as limiting for cyanobacteria growth (Whitton & Potts 2000). Table 3 shows total phosphorus in the groundwater was significantly ($P < 0.05$) correlated with *L. majuscula* photosynthesis ($r = 0.28$); accounting for 8% of the variation in response. This positive correlation agrees with previous laboratory studies where phosphorus additions have been shown to enhance photosynthesis, growth and nitrogen fixation rates of cultured (Elmetri & Bell 2004) and field collected (Kuffner & Paul 2001; Ahern *et al.* 2007a) *L. majuscula*. In-situ field experiments at two locations in Moreton Bay have also demonstrated stimulation of *L. majuscula* growth from phosphorus additions (Ahern *et al.* 2007a; Ahern *et al.* 2008).

Total phosphorus was strongly ($r = 0.65$) and significantly ($P < 0.001$) correlated with phosphate concentrations, but phosphate itself did

Table 3. Correlation matrix of relative photosynthetic response of *L. majuscula* to groundwater nutrient concentrations/properties and correlations between those properties. Values in bold are significant at $P < 0.05$.

Property	Relative *Lyngbya* response	pH	Cond.	Total Fe	Ferrous Fe	Total P	Phos p.	Total N	NH$_4^+$	NO x
pH	0.13									
Conductivity	**0.50**	**−0.25**								
Total iron	**0.53**	**− 0.35**	**0.50**							
Ferrous iron	0.13	−0.24	0.07	**0.61**						
Total phosphorus	**0.28**	0.09	0.03	0.11	0.17					
Phosphate	0.00	−0.05	−0.15	0.02	0.23	**0.65**				
Total nitrogen	0.07	0.05	0.05	0.23	**0.34**	**0.50**	**0.52**			
Ammonium	**0.42**	−0.20	**0.47**	**0.55**	0.38	0.18	0.12	**0.40**		
NOx	**− 0.30**	0.00	0.00	**− 0.41**	−0.28	−0.10	0.09	−0.07	−0.09	
DOC	−0.04	−0.05	0.00	0.16	0.20	**0.46**	**0.56**	**0.55**	0.14	0.03

not significantly correlate (r = –0.004) with the *L. majuscula* photosynthetic response. This anomaly may be due to either adsorption of phosphate on freshly precipitated iron hydroxyoxides, or direct reaction of the phosphate with iron to form insoluble iron phosphate (Menon *et al.* 1990; Chiswell *et al.* 1997) under the circumneutral pH of partially aerated seawater. The total phosphorus would have included organically complexed phosphorus which was probably the available form during the 5 days of the bioassay.

Nitrogen. Nitrogen is an essential macronutrient for growth of marine organisms. There was a highly significant (P < 0.001) correlation (r = 0.42) between ammonium and *L. majuscula* photosynthetic response; with ammonium accounting for 18% of the variation. Although *L. majuscula* is capable of high nitrogen fixation rates (Lundgren *et al.* 2003; Elmetri & Bell 2004) and thus not reliant on an inorganic nitrogen supply from the water column or sediments, nitrogen fixation is energetically expensive, and autotrophic cyanobacteria preferentially uptake inorganic nitrogen from the surrounding seawater (Paerl *et al.* 1987). Cyanobacteria prefer to acquire nitrogen in the form of ammonium (Tandeau de Marsca 1993) as assimilation of nitrate or nitrite requires reduction (via nitrate and nitrile reductase enzymes) to ammonium (Oliver 2000). The addition of inorganic nitrogen has been shown to stimulate *L. majuscula* growth under both laboratory and *in situ* field conditions (Ahern *et al.* 2007a; Ahern *et al.* 2008).

There was a significant (P < 0.05) negative correlation (r = –0.30) of the oxidised inorganic nitrogen form (NOx) and *L. majuscula* photosynthetic response. This is likely because ammonium ions tend to dominate under reducing conditions (common in groundwaters), while nitrate and nitrite ions are more prevalent under oxidising conditions (more common with surface waters). The current study supports this view because ferrous iron in the groundwaters (the common form of iron under reduced conditions) was positively correlated (r = 0.38; P < 0.01) with ammonium, but negatively correlated (r = –0.28; P < 0.05) with NOx (Table 3).

Dissolved Organic Carbon. It has been hypothesised that dissolved organic carbon (DOC) acts as a chelator maintaining iron solubility during transport to bloom sites (Albert *et al.* 2005). Rose & Waite (2003) showed that the formation of iron-organic complexes result in considerably higher, and more persistent concentrations of bioavailable iron and phosphorus in the water column. However, in the current study DOC concentration in the groundwater was not shown to be significantly correlated (r = –0.04) with *L. majuscula* response. This suggests that the measurement of the DOC concentrations alone is not useful for predicting *L. majuscula* response, and the situation is much more complex.

O'Sullivan (2003) found a diverse array of natural organic complexers in the soils, groundwaters and waterways of the Deception Bay study area. Organic matter from different areas was shown to have different complexing strengths, with that from pine plantations being a very strong iron chelator (Rose & Waite 2003). The ability of organic material to complex iron and keep it soluble/bioavailable at higher pH (such as seawater at about pH 8) under aerated or partially oxidising conditions, is the main reason for interest in DOC. In this large dataset with a wide range of vegetations and soils, there was no significant relationship between DOC and ferrous or total iron. In contrast to iron, DOC was significantly (P < 0.01) correlated with phosphate (r = 0.56), total nitrogen (r = 0.55) and total phosphorus (r = 0.46).

pH. Groundwaters pH was not significantly (P > 0.05) correlated (r = 0.13) with *L. majuscula* response. As expected, pH was negatively (P < 0.01) correlated (r = –0.34) with total iron. Iron is more mobile and soluble under lower pH (acidic) conditions (Byrne & Kester 1976; Liu & Millero 2002). Additionally, ASS that have been partially oxidised are acidic, and release iron as a by-product of the oxidation of iron sulfide. The pH of a soil and groundwater have been shown to influence the solubility of nutrients, with both iron and phosphorus minerals generally being more soluble under acidic conditions (McKenzie *et al.* 2004). However, a soil or groundwater with a low pH does not necessarily mean high levels of soluble nutrients. On Bribie, for example, the Podosol soils are highly acidic but the groundwaters are relatively low in total iron because there is minimal iron source in the

highly leached Pleistocene sands, with iron coatings on the sand grains long since removed (Farmer *et al*. 1983).

Conductivity. Electrical conductivity (an indicator of salinity) of the groundwater had a strong and highly significant correlation (r = 0.50) with *L. majuscula* response. Given that the groundwater solutions were diluted at a 1:19 ratio with filtered seawater in the bioassays, the conductivity of the groundwaters is unlikely to have directly affected photosynthetic response in the bioassay. The strong correlation is probably because groundwaters from ASS areas are known to produce significant *L. majuscula* responses (Ahern *et al*. 2006a), but also have higher conductivity. The low pH and high iron concentrations of the groundwaters from ASS areas are also reflected in the negative correlation (r = –0.25; *P* < 0.05) of conductivity with pH, and the positive correlation with total iron (r = 0.50; *P* < 0.001).

Complexity and interactions. The complexity of the nutrient status in groundwater means that its make-up is likely to be unique for any given parcel of land, and extrapolation over an area of more than 1200 km² (Fig. 1) is not useful. However, total iron, total phosphorus and ammonium are important to the *potential* of an area to export nutrients important for *L. majus-*

cula growth, but this potential may be modified or enhanced by the pH and DOC of the groundwater or soil.

THE TEN LANDUSE/VEGETATION/SOIL GROUPINGS

To discover any common reasons for photosynthetic *L. majuscula* responses, the present study investigated the nutrient composition and properties of groundwaters (Fig. 2) from 10 landuse/vegetation/soil groupings (Table 1) which were tested in *L. majuscula* biological assays in Ahern *et al*. (2006a). Analyses of variance showed significant differences between the '10 groups' for pH, conductivity, ferrous iron, total iron, phosphate, ammonium, NOx and DOC (Table 4; Fig. 2). Ahern *et al*. (2006a) found groundwaters from three groups, i) *Melaleuca* on ASS, ii) 'disturbed' on ASS, and iii) *Casuarina* on ASS, produced the most significant (*P* < 0.0001) *L. majuscula* photosynthetic responses (mean ratios 1.8, 1.8, 2.2 times the control respectively; Fig. 2i). The present study has found these three groups share a low pH (means 4.5 ± 0.44; 4.9 ± 0.47; and 4.9 ± 0.56 respectively; Fig. 2ii); very high total iron (means 107 ± 65; 30 ± 15; 54 ± 30 mg L⁻¹ respectively; Fig. 2 v); and very high ferrous iron concentrations (means 42 ± 24; 37 ± 17; 40 ± 19 mg L⁻¹ respectively). The means for

Table 4. One-way ANOVA of nutrient concentrations/properties of groundwaters collected from the 10 landuse/vegetation/soil systems, dominant vegetation, soil order and geology groups in the Deception Bay/Bribie Island study area. Values in bold are significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS non-significant.

Water property	Units	Ten Landuse/ vegetation/soil systems	Soil orders	Vegetation	Geology
pH		$F_{9, 64} = 2.4$*	$F_{4,53} = 2.9$*	$F_{5,68} = 0.9$NS	$F_{2,71} = 7.7$***
Conductivity	μS cm⁻¹	$F_{9, 64} = 15.6$****	$F_{4,53} = 3.7$*	$F_{5,68} = 8.1$****	$F_{2,71} = 14.7$****
Total iron	mg L⁻¹	$F_{9, 64} = 4.3$***	$F_{4,53} = 3.2$*	$F_{5,68} = 2.4$	$F_{2,71} = 11.0$****
Ferrous iron	mg L⁻¹	$F_{9, 64} = 3.8$***	$F_{4,44} = 7.6$****	$F_{5,58} = 1.2$NS	$F_{2,71} = 3.9$*
Total phosphorus	mg L⁻¹	$F_{9, 62} = 1.7$NS	$F_{4,51} = 0.6$NS	$F_{5,66} = 0.8$NS	$F_{2,71} = 0.1$NS
Phosphate	mg L⁻¹	$F_{9, 64} = 2.2$*	$F_{4,53} = 3.5$*	$F_{5,68} = 2.4$*	$F_{2,71} = 2.0$NS
Total nitrogen	mg L⁻¹	$F_{9, 62} = 1.5$NS	$F_{4,51} = 0.4$NS	$F_{5,66} = 0.4$NS	$F_{2,71} = 4.8$*
Ammonium	mg L⁻¹	$F_{9, 64} = 3.4$**	$F_{4,53} = 0.1$NS	$F_{5,68} = 2.6$*	$F_{2,71} = 3.5$*
NOx	mg L⁻¹	$F_{9, 64} = 2.2$*	$F_{4,53} = 0.8$NS	$F_{5,68} = 1.8$NS	$F_{2,71} = 0.8$NS
DOC	mg L⁻¹	$F_{9, 63} = 8.5$****	$F_{4,52} = 2.4$NS	$F_{5,67} = 3.4$**	$F_{2,71} = 3.7$*
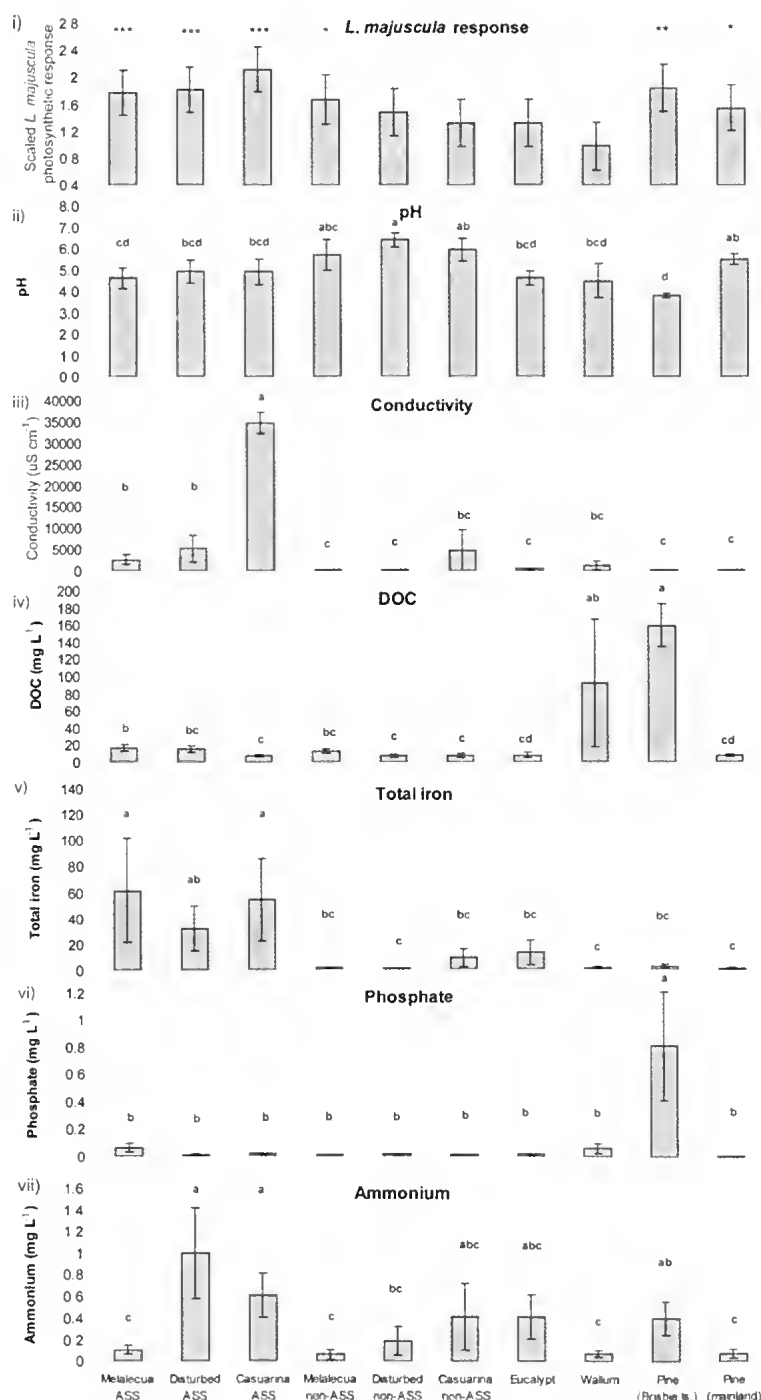
FIG. 2. Mean (±SE) of nutrient concentrations/properties of the groundwaters collected from the '10 landuse/vegetation/soil systems' in the Deception Bay/Bribie Island study area: (i) *L. majuscula* scaled response relative to the control (1.0 = control); (ii) pH; (iii) conductivity; (iv) DOC; (v) total iron; (vi) phosphate; and (vii) ammonium. Level of significant difference of *L. majuscula* response compared to the control mean is shown by * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. For the remaining graphs (ii to vii) means followed by a common letter are not significantly different at $P > 0.05$.

conductivity on these ASS are also high (2700 ± 1100; 4700 ± 2900; 35000 ± 2500 μS cm^{-1} respectively).

Ahern *et al.* (2006a) also found that groundwaters from '*Melaleuca* non-ASS' ($P < 0.05$), 'pine plantations from Bribie Island' ($P < 0.01$) and 'pine plantations from the mainland' ($P < 0.05$) resulted in significantly higher *L. majuscula* responses than the control by 1.7, 1.9 and 1.6 times respectively (Fig. 2i). Waters from these three groups were characterised by low pH (5.7 ± 0.62; 3.8 ± 0.10; and 5.5 ± 0.25; Fig. 2ii) and very low conductivity (210 ± 64; 310 ± 58; 140 ± 23μS cm^{-1}; Fig. 2 iii). 'Pine from Bribie Island' had relatively high mean total phosphorus (0.55 ± 0.31 mg L^{-1}) and phosphate concentrations (Fig. 2vi), probably as a result of fertiliser application at planting. However, mean total phosphorus concentrations in groundwaters from 'pine on the mainland' (mean 0.046 ± 0.006 mg P L^{-1}) were a tenth of that on Bribie. Bribie commonly has impermeable coffee rock layers resulting in perched watertables (Armstrong & Cox 2002). The '*Melaleuca* non-ASS' also had low phosphorus (mean total P = 0.068 ± 0.044 mg L^{-1}; Fig. 2vi). The total iron concentrations of the above three groups were low (means 1.3 ± 0.43; 2.7 ± 1.3; 1.1 ± 0.55 mg L^{-1}) with virtually all total iron present in the ferrous form.

ACID SULFATE SOILS VERSUS NON-ACID SULFATE SOILS

Acid sulfate soils contain significant amounts of iron sulfides, formed by bacterial reduction in water-logged anaerobic conditions when seawater (or sulfate-rich water) mixes with sediments containing iron and organic matter. Very acidic soil solutions and groundwaters are common in ASS areas because when these soils are exposed to air during drainage or disturbance, they oxidise to produce sulfuric acid and various iron compounds. The term ASS also includes soils that have partially oxidised to produce very acidic soils with pH <4.

The mean pH of groundwater from ASS areas in our study (4.75) was significantly ($P < 0.01$) lower than from non-ASS areas (6.04) (Table 5). We found mean total iron concentrations (67 ± 27 mg L^{-1}) in groundwaters from ASS areas were significantly ($P < 0.0001$) and substantially higher (18 times) than the mean from the non-

ASS areas (3.8 ± 2.5 mg L^{-1}). Mean ferrous iron concentration from ASS areas was also 11 times higher than from non-ASS areas, but the difference was not significant ($P > 0.05$). When only ASS groundwater sites are considered, there was a highly significant, strong negative correlation between pH and ferrous iron ($r_{26} = -0.63$) as well as pH and total iron ($r_{26} = -0.61$), showing that higher iron levels were associated with the most acidic groundwaters. The ferrous iron and total iron concentrations of groundwaters from ASS areas were also highly correlated ($r_{26} = 0.87$).

Strongly acidic soils solutions can dissolve insoluble soil minerals, supplying soluble nutrients including phosphorus, nitrogen and trace elements to the soil solution and ultimately the groundwater. Certainly, in the present study mean total phosphorus concentrations were 2.2 times and significantly ($P < 0.05$) higher in groundwaters from ASS areas compared with non-ASS areas (Table 5). Mean phosphate concentrations were also 3.4 times higher in the ASS areas but the difference was not significant due to higher variability. Similarly, the mean total nitrogen and ammonium concentrations were higher (by 1.6 and 2.2 times respectively) in the groundwaters from ASS compared with non-ASS, though the difference was only significant for total nitrogen ($P < 0.05$).

The formation of coastal ASS in a marine environment was reflected in the high salinity (mean EC 12660 ± 2850 μS cm^{-1}) of the ASS groundwater samples. The conductivity of the waters from ASS areas was substantially (6.7 times) and significantly ($P < 0.0001$) higher than the equivalent non-ASS (Table 5).

Ahern *et al.* (2006a) reported groundwaters from ASS areas resulted in significantly higher *L. majuscula* photosynthetic responses compared to non-ASS areas (based on an analysis of a subset of 46 sites from the three groups — *Melaleuca*, 'disturbed', and *Casuarina*). Thus the low pH, high iron and higher phosphorus and nitrogen concentrations in the groundwaters from ASS areas appear very favourable to *L. majuscula* growth. The mix of dissolved nutrients in acid solution can easily be transported into waterways via groundwater flow following rainfall events (Sammut *et al.* 1996; Powell & Martens 2005). Given that ASS in the study area

Table 5. Mean (±SE) and one-way ANOVA of nutrient concentrations/properties of groundwaters collected from ASS and non-ASS areas in the Deception Bay/Bribie Island study area. Values in bold are significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS non-significant.

Water property	unit	ASS areas	Non- ASS areas	F statistic
pH		**4.75 ± 0.27**	**6.04 ± 0.26**	$F_{1,45} = 9.4$**
Conductivity	µS cm^{-1}	**12700 ± 2850**	**1890 ± 1640**	$F_{1,45} = 17.7$****
Total iron	mg L^{-1}	**67.0 ± 27.0**	**3.79 ± 2.45**	$F_{1,45} = 21.6$****
Ferrous iron	mg L^{-1}	37.1 ± 11.8	3.36 ± 2.22	$F_{1,45} = 3.5$NS
Total phosphorus	mg L^{-1}	**0.13 ± 0.035**	**0.06 ± 0.013**	$F_{1,45} = 4.8$*
Phosphate	mg L^{-1}	0.03 ± 0.010	0.01 ± 0.001	$F_{1,45} = 1.1$ NS
Total nitrogen	mg L^{-1}	**1.32 ± 0.21**	**0.81 ± 0.23**	$F_{1,45} = 4.3$*
Ammonium	mg L^{-1}	0.52 ± 0.15	0.24 ± 0.11	$F_{1,45} = 2.5$ NS
NOx	mg L^{-1}	0.23 ± 0.21	0.80 ± 0.48	$F_{1,45} = 4.0$ NS
DOC	mg L^{-1}	13.68 ± 1.96	8.82 ± 1.25	$F_{1,45} = 2.9$ NS

commonly occur on the low-lying Holocene sediments immediately on/or adjacent to the coastline and waterways, drainage or disturbance of ASS areas would rate as a very high hazard for potentially increasing nutrients to *L. majuscula* bloom areas.

These results confirm the very high hazard rating given to iron and pH in the ASS coverage of the nutrient Hazard Model (Pointon *et al.* 2008). A high hazard rating for phosphorus, nitrogen and organics was used for actual ASS associated with wetlands while a medium hazard rating was used for phosphorus, nitrogen and organics for actual ASS not associated with wetlands (Table 4 in Pointon *et al.* (2008)).

VEGETATION

The groundwater data were grouped and analysed by dominant vegetation as land managers commonly use vegetation to discriminate differing land. Analyses of variance showed significant differences between vegetation types for groundwater conductivity, and concentrations of total iron, phosphate, ammonium and DOC (Table 4; Fig. 3).

Melaleuca. The *Melaleuca* communities of the study area (predominantly *M. quinquenervia*) typically occur in low lying areas, ranging from ephemeral wetlands to freshwater swamps. The wet and seasonally reducing conditions found in the soils of *Melaleuca* communities are favourable for the chemical reduction and cycling of

iron and other nutrients (Johnston *et al.* 2003). In Florida, USA, blooms of *L. majuscula* have also occurred adjacent to large freshwater *Melaleuca* forests that yield dark stained waters (J. Burns, pers. comm.). Surface and shallow groundwaters from *Melaleuca* areas commonly have a distinctive dark 'tea' colour (Armstrong & Cox 2002), but despite this, the mean DOC concentration of waters from *Melaleuca* sites in our study areas (16 ± 2.9 mg L^{-1} C) was not as high as from wallum and pine areas (Fig. 3iii). The considerable organic matter/litter found in the surface soil below *Melaleuca* communities should contribute to complexation of iron. In our study, groundwaters from ASS *Melaleuca* sites were characterised by very low pH (mean 4.8 ± 0.38 mg L^{-1}), and the highest total iron (81 ± 50 mg L^{-1}) and ferrous iron (32 ± 19 mg L^{-1}; Fig. 2) concentrations of all vegetation groups, although this was not true of the non-ASS *Melaleuca* sites. Ahern *et al.* (2006a) found groundwaters from *Melaleuca* on both ASS ($P < 0.0001$) and non-ASS ($P < 0.05$) areas significantly stimulated *L. majuscula* productivity by 1.8 and 1.7 times the control respectively. The presence of *Melaleuca* communities in low-lying coastal areas close to waterways, combined with the lower pH and high total and ferrous iron concentrations in their groundwaters, makes such areas a likely source of nutrients to *L. majuscula* blooms.

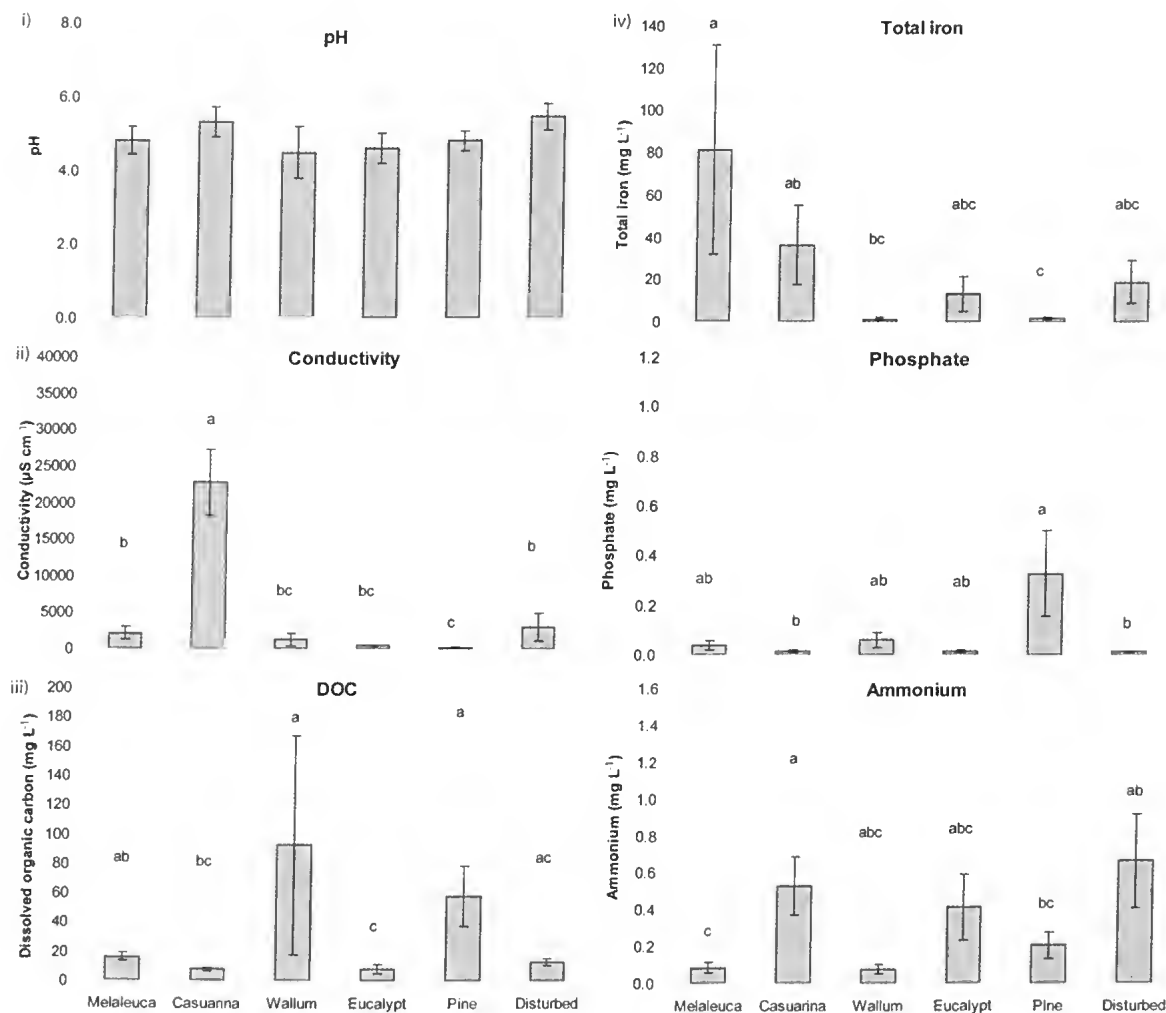**Casuarina.** Groundwaters from *Casuarina* communities were very saline (mean EC 22700 ±

FIG. 3. Mean (±SE) of nutrient concentrations/properties of the groundwaters collected from different vegetations and disturbed landuse in the Deception Bay/Bribie Island study area : (i) pH; (ii) conductivity; (iii) DOC; (iv) total iron; (v) phosphate; and (vi) ammonium. Means followed by a common letter are not significantly different at $P > 0.05$. ANOVA for pH was not significant ($P > 0.05$).

4500 µS cm⁻¹), and had substantially higher ($P <$ 0.05) conductivity than all the other vegetation classes (Fig. 3ii), reflecting their coastal locations close to watercourses and foreshores. These groundwaters were also characterised by low mean pH (5.3 ± 0.40) and relatively high mean total iron (36 ± 19 mg L⁻¹) and ferrous iron (27 ± 12 mg L⁻¹) concentrations, being second only to *Melaleuca* (Fig. 3). Ahern *et al.* (2006a) found that *Casuarina* on ASS (dominantly *C.glauca*), produced a highly significant *L. majuscula* response 2.2 times the control, whereas the non-ASS *Casuarina* (dominantly *C.cunninghamiana*) caused

a response 1.5 times the control but was not statistically significant. The higher response for the *Casuarina* on ASS is likely due to lower mean pH (by a whole unit which is a factor of 10), 6 times higher mean total iron, 5 times higher ferrous iron, 1.8 times total phosphorus, 2.8 times phosphate and 1.5 times ammonium concentrations in the groundwaters, compared with *Casuarina* on non-ASS (Fig. 2).

Wallum. The wallum group (or coastal heath-land) was the only group that did not elevate *L. majuscula* response compared to the control.

Wallum typically grows on acidic, highly leached, sandy, low-fertility soils, deficient in phosphorus and most trace elements (Coaldrake 1961). This was reflected in the groundwaters of the current study, which were very acidic (pH 4.48 ± 0.70) and had very low mean total iron (1.3 ± 0.74 mg L^{-1}), ferrous iron (1.7 ± 0.75 mg L^{-1}), total phosphorus (0.037 ± 0.005) and ammonium concentrations (0.07 ± 0.03 mg L^{-1}) (Fig. 3). Wallum groundwater had high DOC concentrations (92.3 ± 74.6 mg L^{-1}) but probably because of the very low nutrient concentrations, this did not elevate *L. majuscula* response.

Eucalypt. Ahern *et al*. (2006a) reported groundwaters from eucalypt communities elevated *L. majuscula* productivity by 1.3 times the control mean, but this was not statistically significant. Eucalypt vegetation is commonly located on more elevated, better drained, landscapes and thus waterlogging with associated anoxia and high nutrient bioavailability would be atypical. In the current study, the groundwaters from eucalypt communities had the lowest (or equal lowest) phosphorus, phosphate, and DOC concentrations of all the vegetation groups (Fig. 3). However, the mean total iron (13± 8.3 mg L^{-1}) and ferrous iron (10 ± 5.4 mg L^{-1}) concentrations in the groundwaters from eucalypt were higher than for the wallum and pine. This was mainly a result of high iron values from two sites which had ASS at depth, as the other six sites had very low total and ferrous iron concentrations. Interestingly, groundwaters from the two eucalypt ASS sites produced very high increases in *L. majuscula* response (1.6 and 2.1 times the control). Had these two sites not been included in the eucalypt group, the mean *L. majuscula* response would likely have been closer to that of control and the walum. Thus, there appears to be no significant nutrient hazard associated with the eucalypt communities except where they grade onto the lower elevations with ASS at depth.

Pine. Ahern *et al*. (2006a) found the groundwaters from both pine groups (Bribie Island and mainland) significantly ($P < 0.01; P < 0.05$) stimulated *L. majuscula* response, with low pH (4.81 ± 0.27), high DOC (58 ± 21 mg L^{-1}) and relatively high total phosphorus (0.23 ± 0.12 mg L^{-1}) and phosphate (0.32 ± 0.32 mg L^{-1}) concen-

trations being probably responsible (Fig. 3). However, groundwaters from Bribie produced a higher response (1.9 times the control, $P < 0.01$), than those from the mainland (1.6 times, $P < 0.05$). In the present study we found that 'pine on Bribie Island' had significantly and substantially higher mean total phosphorus (15.6 times), phosphate (100 times), nitrogen (4.3 times) and ammonium (5.4 times) concentrations compared to 'pine on the mainland' (Table 6). Another study (Driscoll 2002) found higher phosphorus concentrations in groundwaters under pine plantation on Bribie compared to adjoining undisturbed 'non-pine' sites, and he suggested this was probably due to fertiliser application at planting. The sandy Podosols beneath the pine plantations on Bribie have high permeability in the upper part of the profile allowing leaching of fertiliser into the often perched shallow groundwaters. The extremely low pH (mean 3.78) also probably contributes to the effective leaching of phosphorus fertiliser into the shallow groundwater. In comparison, 'pine on mainland' had a mean pH 1.7 units higher. Very low pH conditions also favour the dissolution and leaching of other soil constituents, such as iron, aluminium and organics. These may form indurated or cemented sand layers (referred to as 'coffee rock') at the relatively shallow depths of the watertable interface. Coffee rock layers are widely distributed on Bribie Island (Armstrong & Cox 2002).

'Pine on Bribie' had 17 times higher mean DOC (133 mg L^{-1}) in the groundwaters than the mainland (Table 6), and were described by Armstrong & Cox (2002) as dominantly 'black' in colour. Such a high DOC is usually associated with shallow perched groundwater over coffee rock (Armstrong & Cox 2002), and this also leads to waterlogging, anoxia, and high nutrient bioavailability. At 'pine on the mainland' sites such indurated layers are uncommon. Organic matter/DOC from pine extracts has been found to have very strong iron complexing properties compared to organics from native vegetations such as *Acacia* and wallum (Rose & Waite 2003). The combination of high rainfall on sandy soils, and the relatively shallow, impermeable layers and perched watertables on Bribie Island, results in lateral movement of shallow groundwaters
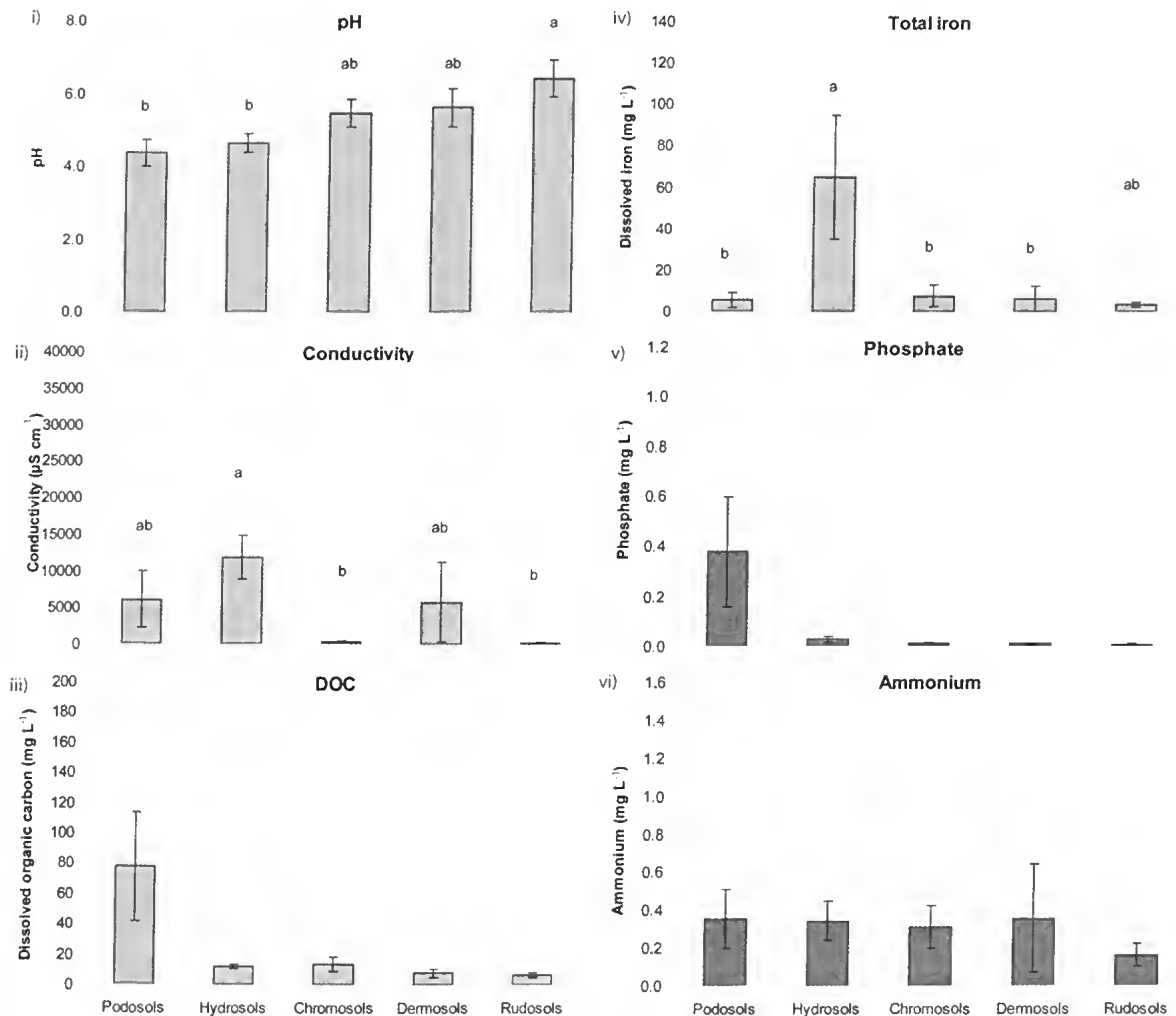
FIG. 4. Mean (±SE) of nutrient concentrations and properties of the groundwaters collected from different soil orders in the Deception Bay/Bribie Island study area: (i) pH; (ii) conductivity; (iii) DOC; (iv) total iron; (v) total phosphorus; and (vi) ammonium. Means followed by a common letter are not significantly different at $P > 0.05$. ANOVA for DOC and ammonium were not significant ($P > 0.05$).

(rich in DOC and phosphorus) into surrounding waterways (Armstrong & Cox 2002). Thus pine plantations (particularly on Bribie), are a potentially important source of nutrients to *L. majuscula* blooms.

SOIL ORDER GROUPINGS

Our study showed highly significant differences in the nutrient concentrations and properties of the groundwaters (Table 4; Fig. 4) from the five main Australian Soil Classification orders (Isbell 1996) in the Deception Bay/Pumicestone Passage area, and thus, consequent differences

in their intrinsic potential to store and supply nutrients needed for *L. majuscula* growth.

Podosols. Podosols are defined as soils with the B horizon dominated by the accumulation of compounds of organic matter, aluminium and/ or iron (Isbell 1996), and include indurated sands or 'coffee rock'. *L. majuscula* has been observed growing on coffee rock where it has been exposed under the sea at Fraser Island (Dennison *et al.* 1999). Groundwaters from Podosols in the current study (Fig. 4) had mean total iron concentration of 5.3 ± 3.5 mg L^{-1} Fe, with a high proportion in the ferrous form (4.9 ± 3.1 mg L^{-1}

Table 6. Mean (±SE) and one-way ANOVA of groundwaters nutrient concentrations/properties collected from pine plantations on the mainland and pine plantations on Bribie Island. Values in bold are significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [NS] non-significant.

Water property	units	Pine (Bribie Is.)	Pine (mainland)	F statistic
Conductivity	µS cm^{-1}	**313 ± 58**	**142 ± 23**	$F_{1,13} = 12.2$**
pH		**3.78 ± 0.10**	**5.49 ± 0.25**	$F_{1,13} = 28.1$***
Total iron	mg L^{-1}	2.73 ± 1.32	1.12 ± 0.55	$F_{1,13} = 1.8$ [NS]
Ferrous iron	mg L^{-1}	2.91 ± 1.22	1.78 ± 0.98	$F_{1,13} = 3.5$[NS]
Total phosphorus	mg L^{-1}	**0.71 ± 0.30**	**0.05 ± 0.006**	$F_{1,13} = 7.0$*
Phosphate	mg L^{-1}	**0.81 ± 0.36**	**0.008 ± 0.002**	$F_{1,13} = 18.7$***
Total nitrogen	mg L^{-1}	**2.81 ± 0.67**	**0.66 ± 0.10**	$F_{1,13} = 8.5$*
Ammonium	mg L^{-1}	**0.40 ± 0.14**	**0.07 ± 0.04**	$F_{1,13} = 11.5$**
NOx	mg L^{-1}	0.05 ± 0.02	0.03 ± 0.02	$F_{1,13} = 2.8$ [NS]
DOC	mg L^{-1}	133 ± 34	7.68 ± 1.3	$F_{1,13} = 3.5$ [NS]

Fe). This is similar to the mean iron levels of other soil orders with the exception of the Hydrosols which had 7 times more ferrous iron and 12 times more total iron than the Podosols. Podosols are commonly highly acidic (Isbell 1996) which was certainly the case in the current study as groundwaters from these soils had the lowest mean pH (4.4 ± 0.35) of all the soil classes in the study area, being significantly ($P < 0.05$) lower than the Rudosols by 2 pH units.

The mean total phosphorus (0.175± 0.036 mg L^{-1}) in groundwaters from Podosols was the highest of all soil orders. The mean phosphate concentrations were significantly ($P > 0.05$) higher than all other soils, but we attribute this to their association with pine plantations that receive fertiliser application at planting. The Podosols also had the highest mean total nitrogen and ammonium values of all the soils, but differences were not statistically significant. Mean DOC concentrations (78 ± 36 mg L^{-1}) were substantially (>5 times) higher than for other soil orders but also not significant ($P > 0.05$), and probably influenced by pine plantation sites (particularly from Bribie) with perched watertables. Perched watertable levels vary widely with season, although the near coastal Podosols, particularly on Bribie, receive more regular top-up from coastal rain. Lateral movement of nutrient-rich perched groundwater via the sandy surface soils to streams and the near shore marine environment, is both likely and of concern.

Hydrosols. Hydrosols include a range of seasonally or permanently wet soils, with saturation of the greater part of the profile for prolonged periods (2–3 months), in most years, necessary for their classification (Isbell 1996). Groundwaters were characterised by high conductivity, very low mean pH (4.6 ± 0.26), and the highest mean total iron (65 ± 30 mg L^{-1}) and ferrous iron (35 ± 12 mg L^{-1}) concentrations of the soil orders (Fig. 4). The significantly higher ($P < 0.05$) mean conductivity (11751 ± 3004 µS cm^{-1}) reflects current or historical marine inundation. The high iron is probably from reducing and oxidative conditions for part of the year, manifested as 'gley' colours and ochrous mottles (Isbell 1996), and many sites are also ASS. As Hydrosols are typically low lying, with groundwaters closer to the surface for at least part of the year, they support more vegetation and have higher nutrient levels than other drier, higher, soil types. Thus, disturbance or drainage of Hydrosols is likely to lead to nutrient export to adjacent waterways.

Chromosols. Chromosols have a strong texture contrast between the topsoil (A horizon) and subsoil (B horizon) (Isbell 1996). In the present study the mean groundwater pH was acidic (pH = 5.45 ± 0.37), while conductivity was very low (197 ± 73 µS cm^{-1}) indicating almost fresh water (Fig. 4). The NOx concentrations were the

highest (mean 10 ± 9 mg L^{-1}) of all the soil orders. Chromosols are predominantly used for agricultural/horticultural production in the study area and so are subject to nitrogenous fertilisation — particularly where pineapples are grown.

Dermosols. Dermosols are soils with structured B2 horizons that lack strong texture contrast between A and B horizons; they also have high agricultural potential with good structure, and moderate to high chemical fertility and water-holding capacity (Isbell 1996). In our study area their groundwaters had a mean pH of 5.6 ± 0.52, similar to the Chromosols (Fig. 4). Mean conductivity was similar to the Podosols at about 0.1 times that of seawater (5740 ± 5420 µS cm^{1-}), but more saline groundwaters occurred closer to the coast.

Rudosols. Rudosols are typically young soils with negligible pedologic organisation, meaning that insufficient time has passed for the colour, texture, or structure of the parent rock or sediments to be significantly modified (Isbell 1996). This was reflected in the low nutrient content of the groundwaters that contained the lowest (or about equal lowest) mean ferrous iron, total iron, phosphate, total phosphorus, ammonium, NOx, total nitrogen and DOC concentrations of all the soil groups (Fig. 4). The mean pH of the groundwaters from these soils was the closest to neutral (6.4 ± 0.5) of all the soils groups, and significantly ($P < 0.05$) higher than the pH of Hydrosols and Podosols. Conductivity was very low (200 ± 73µS cm^{-1}) indicating nearly fresh water.

GEOLOGY

Analyses of variance of the groundwaters from the three main geology groupings [marine, alluvium and continental] sampled in the Deception Bay/Pumicestone Passage area, showed significant differences between groups for conductivity, pH, ferrous iron, total iron, ammonium nitrogen, total nitrogen and DOC (Table 4; Fig. 5).

The marine group had mean groundwater conductivity 38 times higher than the alluvium group (significant at $P < 0.001$), and 68 times the continental group (Fig. 5) , reflecting strong residual salinity from their marine origin. The continental group, with the lowest mean conductivity, consists mainly of the *Landsborough Sandstone* formation originally formed from the

accumulation of terrestrial sediments (where the salt content of the sandstone was inherently low). Though the alluvium group also had higher mean conductivity than the continental group, this was not statistically significant.

The marine group had much lower mean pH (4.61 ± 0.2) than the continental group (5.46 ± 0.32) and significantly ($P < 0.001$) so for the alluvium group (pH= 5.98 ± 0.24) (Fig. 5). The very low mean pH of the marine group is mainly attributed to areas with oxidation of iron sulfide in the ASS common to this group (though potential ASS that has not begun to oxidise, or is under the tidal influence of sea-water, would be expected to be similar to sea-water i.e. neutral to slightly alkaline). Other very low pH soils in this group include the coastal sandy soils (mainly Podosols) supporting pine plantations on Bribie Island.

The mean ferrous iron concentration from the marine areas was significantly ($P < 0.01$) greater (8.6 times) than the alluvium group, and 22 times greater than the continental group, though not significant on the latter. The mean total iron concentration of the Marine group was significantly ($P < 0.001$) greater (18 times) than the alluvium group, and 35 times greater than the continental group ($P < 0.05$). The ASS in the marine group are largely responsible for these higher iron concentrations.

The mean ammonium concentration of the marine group was significantly ($P < 0.05$) higher than the continental group (by 4.9 times), and almost double that of the alluvium group though this was not significant. The mean NOx levels of the marine group was less than a third of the other two groups, although all levels were quite low (Fig. 5). This suggests that the groundwaters from the marine group usually experience lower redox conditions than the other groups. Marine group soils are usually located in the lowest landscape positions, and many sites (particularly with ASS) may be water-logged for at least a few months of the year — hence more reduced than the better drained alluvium and continental groups. The mean total nitrogen of the marine group was significantly ($P < 0.01$) greater (2.8 times) than the alluvium group, and 1.6 times the continental group, though not significant for the latter.
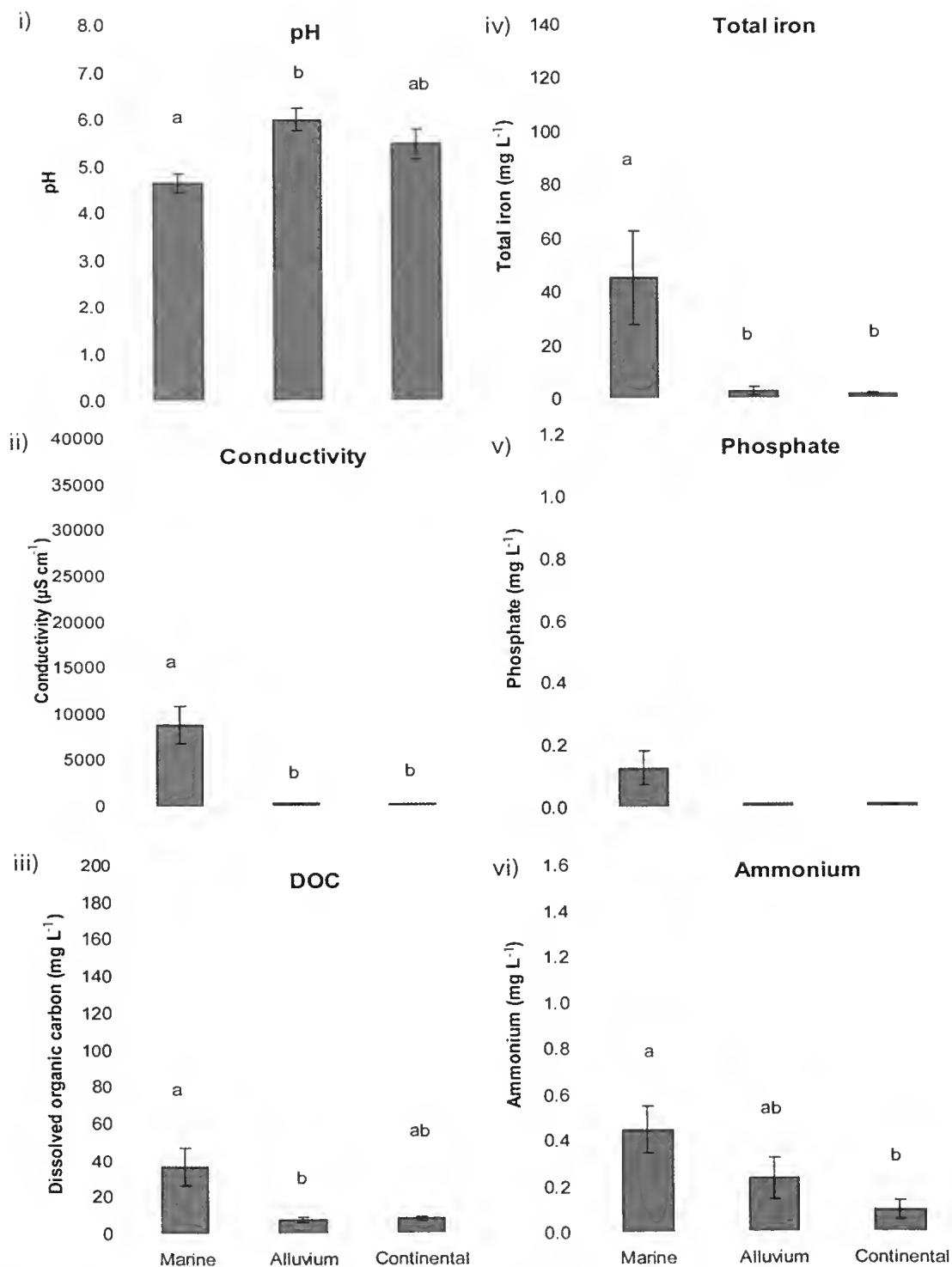
FIG. 5. Mean (±SE) of nutrient concentrations and properties of the groundwaters collected from different geologies in the Deception Bay/Bribie Island study area: (i) pH; (ii) conductivity; (iii) DOC; (iv) total iron; (v) total phosphorus; and (vi) ammonium. Means followed by a common letter are not significantly different at $P > 0.05$.

APPLICATION FOR MODELLING

The outcomes of the present study confirm the efficacy of the *Lyngbya majuscula* nutrient 'Hazard Model', support its further refinement, and assist with hazard ratings. This model was created to identify, and rate, different areas, in terms of how likely/vulnerable they are to supply and export nutrients that could increase the likelihood and magnitude of *L. majuscula* blooms in southeast Queensland (Pointon *et al.* 2008). The map outputs from earlier versions of the Hazard Model have helped to identify areas needing further assessment (EPA 2006). The eventual aim is to incorporate nutrient hazard maps into local government planning schemes.

NUTRIENTS AND PROPERTIES

Increases in iron and phosphorus were directly and significantly correlated with *L. majuscula* photosynthetic response, and both were significant dependant variables in the multiple regression. Thus our data support the inclusion of both nutrients in the risk-rating process. This is further supported by other laboratory and *in situ* studies that have shown similar responses to additions of organically chelated iron (Gross & Martin 1996; Dennison *et al.* 1999; Ahern *et al.* 2006b) and/or phosphorus (Kuffner & Paul 2001; Elmetri & Bell 2004; Ahern *et al.* 2007a).

The inclusion of pH in the risk-rating process is also supported. Groundwater pH was a significant dependant variable in the multiple regression of *L. majuscula* photosynthetic response. pH was initially included in the hazard rating process of the Hazard Model because of its known affect on the solubility and hence the movement and bioavailability of iron and phosphorus. In this study, the generally greater solubility of iron with low pH led to a negative correlation between total iron and pH, i.e. the more acidic waters generally had the highest total iron contents.

With regard to nitrogen, the significant correlation of *L. majuscula* productivity with ammonium concentrations supports its inclusion in the Hazard Model. However, despite being shown in this and other studies (Ahern *et al.* 2007a; Ahern *et al.* 2008) that growth is stimulated by additions of inorganic nitrogen, *L. majuscula*

can also fix atmospheric nitrogen (Lundgren *et al.* 2003), and is therefore not necessarily completely reliant on an external inorganic nitrogen source.

The results for dissolved organic carbon emphasise the complex relationships between DOC and *L. majuscula* response, especially when different organic sources of DOC are involved. While there were significant correlations of DOC with total nitrogen, total phosphorus, and phosphate, measuring the concentrations of DOC alone, without measuring the strength of complexing properties was not predictive of a *L. majuscula* response. None-the-less, the inclusion of DOC in the Hazard Model is partly justified given that DOC (sourced from the Deception Bay/Pumicestone Passage catchment) has been shown to strongly complex iron and thus reduce its precipitation in seawater (Rose & Waite 2002; Rose & Waite 2003). Measurement of the DOC complexing strength with iron (and phosphorus) for a much wider range of landuses/vegetation/soil/geology in the catchment, may improve its usefulness in the Hazard Model, as only a limited number of organic sources have been tested for complexing strength (Rose & Waite 2002; Rose & Waite 2003).

Although conductivity was a significant dependant variable in the multiple regression, any suggestion that it would directly cause an *L. majuscula* response is unsupported, and there is no justification for its inclusion in the Hazard Model.

VEGETATION, SOILS, GEOLOGY AND LANDUSES AS SIMPLE RISK IDENTIFIERS

Some areas within the catchment characterised by differing vegetation, soils, geology and landuse, also differ in their potential to supply nutrients to the waterways. Areas with ASS, *Melaleuca* vegetation, pine plantations, *Casuarina* on ASS, Hydrosols, Podosols and 'marine influenced geology' all have groundwaters that directly increase *L. majuscula* response in bioassays, or that contain significant quantities of nutrients likely to cause this response. The importance of careful management of such recognisable parcels of land should be communicated to landholders, particularly as it does not require the more complex explanations associated with the Hazard Model.

In addition, areas with some of the following characteristics may be important contributors of nutrients to *L. majuscula* blooms if subject to disturbance or alteration, and should be rated medium to high hazard in the Hazard Model:

• Areas that contain appreciable concentrations of iron, phosphorus and/or nitrogen, or where management involves application of organic or inorganic fertilisers;

• Areas where site conditions (e.g. waterlogging and anaerobic conditions, perched groundwater tables) promote formation of nutrients into bioavailable form;

• Areas where the site conditions readily promote transport of nutrients to waterways (e.g. highly transmissive, permeable soils with perched watertables, such as Podosols on Bribie).

Obviously, if such areas are also situated close to waterways and coastlines (e.g. ASS areas, *Melaleuca* wetlands), they are likely to be a still greater hazard. This was taken into account in the Hazard Model by the use of proximity to coast and streams layers.

A limitation of the current study was that it could only test and examine groundwaters from a limited number of different landuses/vegetations/soils combinations. Although those combinations tested were very relevant, as they included many 'higher risk' practices as well as spatially extensive areas of the catchment (e.g. pine plantations), further testing of other combinations of soils, vegetations and landuses present in the study area are needed. Furthermore, more testing is required when extending the Hazard Model beyond the 'reference area' used in this study to other coastal areas of Southeast Queensland.

ACKNOWLEDGEMENTS

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Modelling land based nutrients relating to *Lyngbya majuscula* (Cyanobacteria) growth in Moreton Bay, southeast Queensland, Australia

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ABSTRACT

Moreton Bay, in southeast Queensland, experiences seasonal blooms of the cyanobacterium, *Lyngbya majuscula*. Mounting evidence suggests nutrients can increase the intensity and severity of *L. majuscula* blooms when environmental conditions are favourable. The main 'nutrients' of concern, are bio-available iron, phosphorus, nitrogen and dissolved organic carbon. The current study used a GIS-based model to generate a map identifying areas most likely to supply/export nutrients of concern to Moreton Bay. Based on GIS coverages (acid sulfate soils, landuse, soils, groundwater, pre-clearing vegetation and remnant vegetation) and a proximity to coasts and streams coverage (to weight the likelihood of export), parcels of land were ranked for hazard and compiled into a nutrient hazard model. The model was initially developed in a reference area (46,000ha) supported by field investigations, soil analyses and *L. majuscula* bioassay and laboratory analysis of groundwaters. The map outputs compared favourably with soil analyses from > 80 sites collected following model development. The model was extended beyond the reference area to produce an indicative nutrient hazard map of coastal Southeast Queensland (2.3 million ha). The model and resulting maps from this investigation provide an areal assessment of where to concentrate efforts to limit or reduce nutrient loads that may contribute to *L. majuscula* blooms. Maps produced from earlier modelling have been used to support a new *Algal Blooms policy 2.4.7* within the *Southeast Queensland Regional Coastal Management Plan* (EPA, 2006) and versions in this paper provide an update. Appropriate nutrient management guidelines need to be developed for industry use when disturbing areas rated high or very high in the nutrient hazard maps. ❏ *acid sulfate soils, bio-available iron, cyanobacteria, dissolved organics, GIS, nitrogen, phosphorus, nutrient hazard map*

Coastal waters worldwide appear to be experiencing an increase in the occurrence of harmful algal blooms (Paerl 1988; Paerl & Fulton 2006). In particular, the cyanobacterium *Lyngbya majuscula* has been causing a nuisance in coastal waters and reef environments worldwide (Dennison *et al.* 1999; Albert *et al.* 2005), including along the coast of Queensland (Albert *et al.* 2005). Blooms in Moreton Bay, have increased in size, frequency and severity since the early 1990's (Dennison *et al.* 1999; Ahern *et al.* 2007b).

Lyngbya majuscula (family Oscillatoriaceae) is a toxic (see review in Osborne *et al.* 2001), filamentous, benthic cyanobacterium that grows in close association with the sediment, or epiphytically on seagrass, macroalgae or corals (Dennison *et al.* 1999). It appears to be a common, non-dominant component of many shallow subtropical and tropical marine ecosystems (Diaz *et al.* 1990) but also can undergo explosive growth and areal expansion forming mono-specific blooms that overgrow and smother intertidal and subtidal benthic communities (Watkinson *et al.* 2005).

The rapid proliferation of cyanobacteria blooms requires the availability of the macronutrients nitrogen (N) and phosphorus (P), and micronutrients including iron (Fe) which regulate photosynthesis and ultimately growth. As *L. majuscula* has the capacity to fix N, it is less likely that growth will be limited by low N availability (Diaz *et al.* 1990; Lundgren *et al.* 2003), as is common for marine plants in many tropical and subtropical environments including Moreton Bay, Queensland (e.g. O'Donohue & Dennison 1997). Instead, laboratory studies have shown P (Kuffner & Paul 2001; Elmetri & Bell 2004; Ahern *et al.* 2007a), bio-available Fe (Gross & Martin 1996; Ahern *et al.* 2006b, 2007a), and to a lesser extent molybdenum (Mo) (Ahern *et al.* 2006b) are important for growth, photosynthesis and N fixation of *L. majuscula*. These results have been confirmed by in-situ field studies in eastern (Ahern *et al.* 2007a) and north-western Moreton Bay (Deception Bay) (Ahern *et al.* 2008a), where prolific growth of *L. majuscula* has resulted when bio-available Fe, P and N were added to the water column.

Organic matter (such as humic and fulvic acids found in runoff from coastal catchments) also appears to play an important role as a chelating agent, complexing and maintaining solubility of Fe and/or P in the slightly alkaline seawater (Rose & Waite 2003). This has the effect of increasing the availability of Fe, and to a lesser extent P, to *L. majuscula* (Ahern *et al.* 2006b). Organic matter formed from pine plantations has shown to be a particularly strong complexor (Rose & Waite 2003).

Soil and groundwater pH can strongly influence the leaching ability and solubility of nutrients, Fe in particular (McKenzie *et al.* 2004), but also most P minerals and compounds are more soluble under acidic conditions. Coastal sandy sediments are commonly acidic and have little ability to retain nutrients. Another soil group, termed acid sulfate soils (ASS), contain iron disulfides, mainly pyrite, and sometimes iron monosulfides that on exposure to air from disturbance or drainage, produce large quantities of acid and Fe. ASS can vary from sand through to fine textured clay and marine muds. The acidic conditions maintain Fe solubility, thus large quantities of Fe can be exported from the area via ground or surface waters. ASS commonly occur along drainage lines or close to the coast, and as they are common in south eastern Queensland their impact on inshore waters can be significant.

Given the rapid population growth along coastal southeast Queensland (Graymore *et al.* 2002), coastal catchment activities must be carefully managed to limit or reduce the supply and transport of bio-available nutrients to waterways and coastal waters. If nutrient inputs continue to increase, then seasonal *L. majuscula* blooms are likely to be larger, and their impacts more severe. Different parts of the catchment have different nutrient compositions and quantities, and vary also in their ability to export/transport bio-available nutrients to waterways and/or groundwaters. Thus the exact sources of nutrients, and the transport pathways to *L. majuscula* bloom sites, need to be accurately determined. The aim of the present study was to create a model that would produce map outputs showing areas that have the potential to supply/export nutrients to coastal waters in southeast Queensland at levels that could accelerate *L. majuscula* growth.

MATERIALS AND METHODS

STUDY AREA

The meso-scale (detailed reference area) modelling and field assessment involved the area (approx. 46,000ha) from Scarborough to Donnybrook. Following the trial of the methodology on the 'reference area' (meso-scale maps) the methodology was extended to the whole area (macro-scale map). The macro-scale (broad scale) modelling encompassed the coastal areas (approx. 2,257,000ha) from the Queensland/ New South Wales border (28°10′ lat.) to Eumundi (26°45′ lat.) and was bounded on the west by the Great Dividing Range. It included the following major catchments: Brisbane River, Logan River, Pine River, Caboolture River, Maroochy River, Mooloolah River and the Pumicestone Passage and Gold Coast catchments.

EXISTING GIS COVERAGES

Multiple GIS coverages (ASS, landuse, soil, groundwater, pre-clearing vegetation, and remnant vegetation) were included in the model to enable integration of different factors (such as soil, vegetation and landuse type) that are known to impact on the ability for different parcels of land to store and/or supply nutrients. Based on current understanding of the nutrients required for *L. majuscula* growth, these GIS coverages were identified as being the best combination to indicate areas of potential nutrient storage and supply. However they have been reinterpretated in this paper to make the parameters specifically apply to modelling of nutrient sources.

An additional GIS coverage was developed to indicate proximity to coasts and streams. Our model could thus take into account both the intrinsic nutrient storage capacity of a particular parcel of land as well as its potential to supply and export those nutrients to estuarine and near coastal environments.

ASS coverage. Macro-scale data were compiled by NRW (Queensland Department of Natural Resources and Water) during a number of projects in the area. Mapping scales range from 1:25 000 to 1:100 000. A rating of 1 was assigned to areas not assessed during ASS survey. The sand islands of Moreton Bay were given a rating depending on the topography and geology, since only limited field-testing of the soils has been carried out. The highest rating of 4 was restricted to actual ASS areas (where field pH is <4.0), due to their known potential to release Fe.

Land use coverage. Digital land use maps as at 1999, at a nominal scale of 1:50 000, were available for the catchments of Brisbane, Logan and Albert Rivers, south coast streams (i.e. Gold Coast), Pine Rivers, Pumicestone Passage rivers and streams (including the Caboolture River), and the Maroochy and Mooloolaba Rivers (NR&M 2005a). Land use is classified according to the Australian Land Use and Management Classification (ALUMC) version 5, November 2001.

Land uses that were given a high rating of 3 or 4 included areas where:

- large amounts of fertiliser are regularly applied, e.g. agriculture.

Table 1. Details of soil surveys used in the GIS 'soil coverage'.

Organisation	Survey study area	Scale
NRM&E	Brisbane Valley land resource survey	1:50 000
NRM&E	Lockyer valley land resource survey	1:50 000
NRM&E	Soils and land suitability — Albert River, Chardons Bridge to Boylands	1:50 000
CSIRO	Soils and land use in the Beenleigh–Brisbane area	1:50 000
CSIRO	Soils of the Brisbane and south east environs	1:50 000
QDPI	Horticultural land suitability survey — Sunshine Coast	1:100 000
QDPI	Moreton region land management field manual	1:100 000
CSIRO	Atlas of Australian soils	1: 2 000 000

Table 2. Broad categories of dominant aquifer material used to develop the groundwater coverage (adapted from Preda & Cox 2004). Hazard ratings for each category for the five nutrients are shown in the last five columns.

	Dominant aquifer material	Hydraulic conduc-tivity (m/day)	Fe content (mg/L)	References	Ratings				
					Fe	P	OC	pH	N
A	Igneous rocks	0.0001			1	1	1	1	1
B	Sandstone	0.01	0–3	Harbison & Cox 2002; Armstrong & Cox 2002; Ezzy *et al.* 2002	2	1	2	1	2
C	Basalt	2.50	0–2	Locsey, 2003; Barclay, 1997	2	1	3	1	3
D	Alluvial sediments adjacent to 2 (>10m AHD)	5.00	0–5	Wilson (unpub. data)	3	1	4	2	4
E	Alluvial sediments adjacent to 3 (>10m AHD)	5.00			3	1	4	2	4
F	Marine deposited sandy sediments (<10m AHD)	6.50	0–20	Armstrong & Cox, 2002	4	1	4	3	4
G	Marine deposited fine-grained sediments (<10m AHD)	0.10	1–35 10s–100s	Harbison & Cox 2002; Ezzy *et al.* 2002; Lee *et al.* 2002	4	1	2	4	2

- frequent soil disturbance occurs, e.g. extractive industries.
- large quantities of nutrients are produced and exported, e.g. sewage treatment plants, intensive agriculture.
- high levels of natural nutrient are present, e.g. coastal wetlands.

General soils coverage. Data from various soil mapping studies undertaken at different times, scales and for different purposes (Table 1) and resulting in mapping products of variable scale, style and data content were reinterpreted to achieve a consistent classification. Soil units were rated according to nutrient concentration and pH, with the many soil units without analytical assessment assigned ratings according to analysis of similar soils in adjoining surveys. Use of different scaled maps resulted in abrupt changes in the polygon size and purity at the map boundaries.

Groundwater coverage. The groundwater coverage (Table 2) assesses the likely hazard of nutrients from the deeper (>3m) groundwater that may seep into Moreton Bay and affect *L. majuscula* productivity. Geological maps (NR&M 2002), elevation data (NR&M 2005b), and data on the Fe content and hydraulic conductivity of the dominant aquifer material were used to assign ratings in the groundwater coverage (Preda & Cox 2004). Porous geological units likely to contain water and Fe-rich minerals (e.g. basalt) were given a high rating while massive rocks with little Fe (e.g. granite) were rated low.

Vegetation coverage. Data came from the Queensland Environment Protection Agency (EPA 1999a, 1999b), and was derived from both pre-clearing and remnant vegetation surveys. The dominant regional ecosystem unit within the attribute table of the vegetation GIS coverages was used for assessment purposes, with ratings assigned to each unit according to previously recorded *L. majuscula* bioassay growth responses, or other available references. Albert *et al.* (2005), Ahern *et al.* (2006a) and Ahern *et al.* (2003) all recorded

Table 3. Proximity ratings for the five nutrients used in the GIS 'proximity coverage'. For a particular nutrient, ratings are a combination of distance from the coast (columns) and distance from streams (rows).

Nutrients			Proximity rating						Moreton Bay Islands
			Distance to coast (km)						
			<5	5 to 10	10 to 20	20 to 30	30 to 50	>50	
Fe	Distance to stream (km)	>1	2	2	1.75	1.5	0.75	0.5	4
		0.5 to 1	3.2	3.2	2.8	2.4	1.2	0.8	
		<0.5	4	4	3.5	3	1.5	1	
OC	Distance to stream (km)	>1	2	2	1.75	1.5	1.1	1	4
		0.5 to 1	3.2	3.2	2.8	2.4	1.76	1.6	
		<0.5	4	4	3.5	3	2.2	2	
P	Distance to stream (km)	>1	1.1	1.1	1	1	0.85	0.75	1.98
		0.5 to 1	1.76	1.76	1.6	1.6	1.36	1.2	
		<0.5	1.98	1.98	1.8	1.8	1.53	1.35	
pH	Distance to stream (km)	>1	1.1	1.1	1	1	0.85	0.75	1.98
		0.5 to 1	1.76	1.76	1.6	1.6	1.36	1.2	
		<0.5	1.98	1.98	1.8	1.8	1.53	1.35	
N	Distance to stream (km)	>1	1.1	1.1	1	1	0.85	0.75	1.98
		0.5 to 1	1.76	1.76	1.6	1.6	1.36	1.2	
		<0.5	1.98	1.98	1.8	1.8	1.53	1.35	

positive *L. majuscula* responses to diluted soil extracts or shallow groundwater taken from vegetation communities containing *Melaleuca*, *Casuarina*, or pine plantations. As a result, regional ecosystems with these species received the highest rating compared to those without these species.

In the early stages of model development, only the remnant vegetation map was used. However, as much of the vegetation in the study area has been cleared, this resulted in a potential bias to the areas where vegetation remains. Therefore, in the current model, both pre-cleared vegetation and remnant vegetation layers were included, with a weighting of 0.5 for each.

Coast and stream proximity coverage. This was developed to allow greater emphasis to be placed on nutrient sources closer to streams and rivers (<0.5km; 0.5–1.0km; >1.0km from streams). Distance from the coast (<5; 5–10; 10–20; 20–30; 30–50; >50km) was included to broadly reflect the distance nutrients had to travel to estuaries and near shore marine locations, and the influence this may have on bio-availability at the destination. These two coverages were used to produce a 'proximity coverage' with values allocated to the combination of categories (Table 3).

Factors affecting nutrient transport and bio-availability are complex, and depend on interactions involving oxidation, pH, salinity, temperature, amount of water mixing, and time. As a result different proximity values (Table 3) were needed for some nutrients. For example, ferrous Fe (the most soluble inorganic form of Fe) rapidly oxidises in aerated water and generally forms precipitates of ferric oxyhydroxides, particularly as acidity decreases. These Fe precipitates may still be transported into estuaries and near-shore marine environments, but studies suggest that precipitated Fe, and the Fe oxides common in particles eroded from soils, are virtually unavailable for uptake by *L. majuscula*. Therefore, lower Fe proximity values were allocated to polygons

Table 4. Some brief examples of attribute tables from four of the GIS coverages, showing the addition of hazard ratings for each of the five nutrients. A rating of 1 is low or unknown, 2 is medium, 3 is high and 4 is very high.

Layer	Attribute code	Description	Nutrient hazard ratings				
			Fe	P	OC	N	pH
Soils	P	Lithosols sandy (Rudosol)	1	1	1	1	1
	W	R-Y podzolics sedimentary (Kurosol)	2	1	1	1	2
	DE	Prairie soil (Dermosol)	3	3	1	3	1
Acid sulfate soils	A0S0	Actual acid sulfate soil	4	2	2	2	4
	A0S0W	Actual acid sulfate soil wetlands	4	3	3	3	4
Land use	3.5.4	Seasonal horticulture, vegetables and herbs	2	3	2	3	2
	5.4.2	Rural residential development	1	2	1	2	1
Vegetation	12.2.7	*Melaleuca quinquenervia* on sand plains	3	1	1	3	3
	12.2.10	*Eucalyptus* sp. and *Corymbia* sp. on dunes and sand plains	3	1	1	3	3

greater than 1 km from a stream and greater than 30 km from the coast, compared to other nutrients (Table 3) that are not subject to the same rapid oxidation effects. For example, most P is adsorbed onto soil particles, which are suspended and later deposited in the marine environment by rainfall events. The proportion of soluble P is usually low except where fertiliser is used. Soluble P is usually longer lived in solution than soluble Fe species.

RESOURCES USED TO ASSIGN HAZARD RATINGS

Literature including maps, analytical reports, journal articles and student theses, along with data from site investigations, provided most of the information used to assign hazard ratings to separate parcels of land. Site investigations involved nutrient analyses from soil cores at 74 sites (although 160 sites have now been completed), and groundwater samples (<3m) also from 74 sites. Most sampling was conducted within the boundaries of the meso-scale hazard map. It was hoped that a detailed understanding of relationships in this smaller area, would allow more accurate macro-scale extrapolation. Where information gaps persisted ratings were assigned using expert opinion. Such ratings were further reviewed and debated by an interdisciplinary group of scientists (Southeast Queensland Healthy Waterways Partnership Scientific Panel).

Analyses were conducted by the NATA registered laboratory of the Natural Resource Sciences Chemistry Centre, NRW, Brisbane. Soils were analysed for pH (1:5 water) (4A1), extractable P (9B2), extractable Fe (12A1_Fe), total carbon (6B4) and extractable N (7B1) (method numbers shown after the test refer to Rayment & Higginson, 1992). Acid sulphate soils were identified by soil profile morphology, peroxide field pH tests (Ahern *et al.* 1998) and laboratory analyses following the ASS methods of Ahern *et al.* (2004).

Shallow (<3m) groundwater samples were collected from piezometers installed by the Queensland Department of Natural Resources and Water (NRW), and analysed for pH (4500H), Electrical Conductivity (EC) (2510A), nitrate (NO_3) N (4500NO3-I), dissolved inorganic carbon (5310A), dissolved organic carbon (5310D), ammonium (NH_4^+) N (4500NH3H), phosphate (PO_4^{3}) P (4500PG) and total N (4500Norg+4500NO3-I) (method numbers shown after the test refer to APHA-AWWA-WPCF, 2005). Statistical analyses of the groundwater analyses are given in an accompanying paper (Ahern *et al.* 2008b).

MODELLING PROCESS

The aim was to calculate a numerical hazard rating for each polygon in the final GIS based model coverage. The extensive modelling process, (summarised in Figs 1 and 2) involved a complex

series of steps. To assist understanding, the steps (for Fe) are detailed below.

Step 1. *Assign Fe hazard rating to attribute table.* Fe hazard ratings are added to the attribute tables of the six coverages (ASS, landuse, soil, groundwater, pre-clearing vegetation and remnant vegetation). Each of the existing GIS coverages was a vector coverage, with its own associated tables containing descriptions and attribute codes for each polygon. Based on the information resources described earlier, and the attribute itself, an individual hazard rating (on a scale of
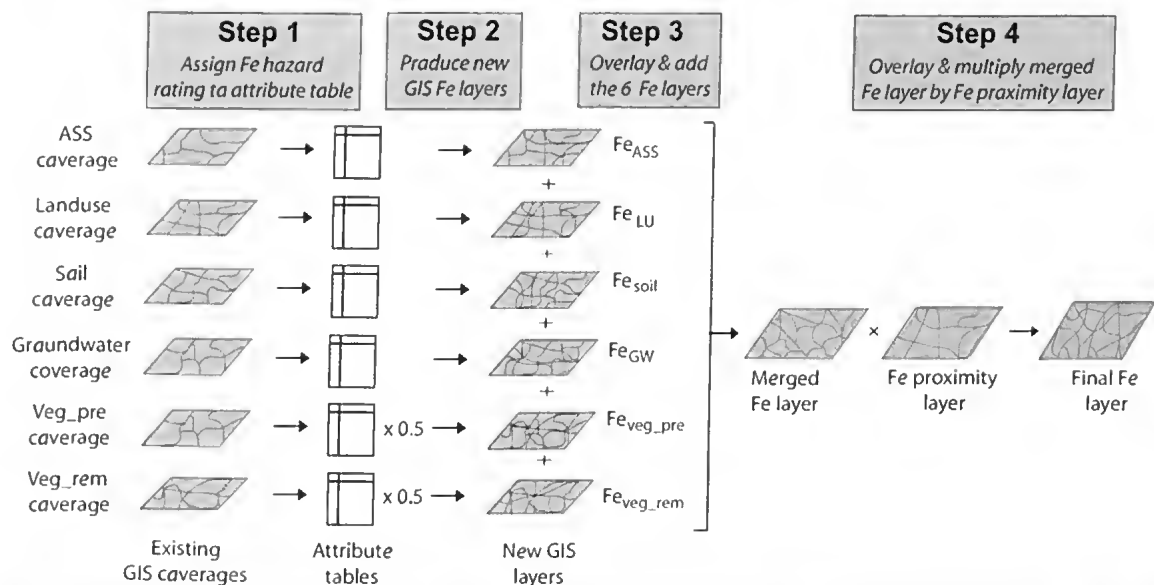

FIG. 1. Diagrammatic representation of steps 1–4 of the nutrient hazard model, (using iron as the example).
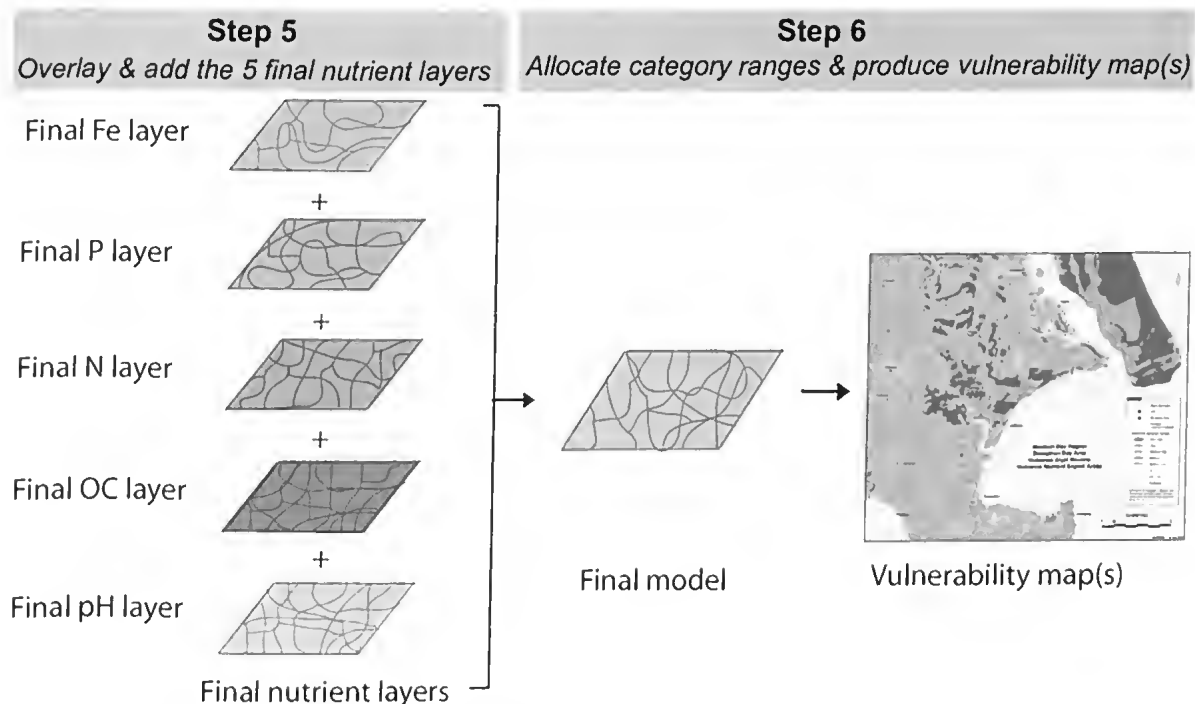

FIG. 2. Diagrammatic representation of steps 5–6 of the nutrient hazard model.

1 to 4) for Fe is allocated to the polygon table to produce an extended attribute table for each coverage (see examples in Table 4). Hazard ratings are based on the potential of a particular parcel of land (polygon) to deliver a nutrient for transport: 1 = low (or unknown); 2 = medium; 3 = high; and 4 = very high (a rating of 4 is restricted to extreme areas, e.g. actual ASS areas where field pH is <4.0).

Step 2. *Produce six new GIS Fe layers.* New Fe coverages are produced for ASS (Fe_{ASS}), landuse (Fe_{LU}), soil (Fe_{Soil}), groundwater (Fe_{GW}), pre-clearing vegetation ($Fe_{Veg-pre}$), and remnant vegetation ($Fe_{Veg-rem}$). These consist of the original polygon boundaries, but with added values of 1 to 4 (taken from the extended attribute table). The software dissolves boundaries between adjoining polygons with the same numeric value to produce a new layer with a reduced number of polygons (Fig. 1). Note the Fe hazard rating in the attribute tables of two vegetation coverages is multiplied by 0.5 to give values of 0.5–2. This gave the overall weighting of 1.0 for the sum of both vegetation coverages as discussed earlier.

Step 3. *Overlay and add the six Fe layers.* A new merged Fe layer is produced by overlaying the six new GIS Fe layers produced in step 2. Boundaries between adjoining polygons with the same numeric value are dissolved to produce a new merged Fe layer.

Step 4. *Overlay and multiply the merged Fe layer and the Fe proximity layer.* The merged Fe layer is overlaid and multiplied by the proximity factor layer for Fe (PF_{Fe}) to produce another Fe layer. Boundaries are dissolved between adjoining polygons with the same numeric value to produce a final Fe layer which thus takes into account all GIS coverages as well as proximity to coasts and streams.

The process described for Fe in steps 1 to 4 is repeated for the remaining four nutrients, resulting in five final nutrient layers (Fe, P, N, OC, pH) that have been merged and multiplied by their corresponding proximity coverage. The program creating the model conducts these steps sequentially once all the hazard ratings are entered in the attribute tables of the initial coverages.

Step 5. *Overlay and add the five final nutrient layers.* The five final nutrient layers (Fe, P, N, OC, pH) are overlaid on each other (Fig. 2) and the values are added to give a new combined nutrient layer. Boundaries are dissolved between adjoining polygons with the same numeric value to produce the 'final model' (a GIS coverage with numeric hazard values for each final polygon).

Step 6. *Allocate category ranges and produce hazard map(s).* Category ranges are allocated in the numeric model. Colours are selected to display each category range and then nutrient hazard maps are produced (Fig. 3).

RESULTS AND DISCUSSION
MESO-SCALE MAP

The map (Fig. 3) highlights that the high and very high nutrient hazard areas (coloured pink and red) generally coincide with actual ASS, potential ASS, pine plantations, soils with elevated Fe concentrations, vegetation communities containing *Melaleuca* and *Casuarina* species, and the highly transmissive sandy soils of Bribie Island and the coastal lowlands. Extensive soil (160 sites) and water (74 piezometers) sampling has been conducted in this area, and while some data were available during the model development phase, most have been produced recently and has been useful to compare with model outputs.

The model output map (Fig. 3) also reflects the results of both the extensive soil sampling program (Pointon *et al.* 2007), and the shallow groundwater sampling (Ahern *et al.* 2008b, this volume), and shows some limited areas of *Melaleuca*, and an appreciable area of pine plantations, as only rated medium high (orange colour Fig. 3). *Algal Blooms* policy 2.4.7 (EPA 2006) only emphasises caution with high and very high categories. Groundwaters and some soil extracts from pine plantations, *Melaleuca* and ASS have shown significant responses when a small amount was added to *L. majuscula* bioassays in seawater (Ahern *et al.* 2006a; Albert *et al.* 2005; Ahern *et al.* 2003). In-situ experiments in Moreton Bay (Ahern *et al.* 2007a) show such laboratory results are transferable to natural situations. Additionally, highly significant *L. majuscula* responses to added Fe, P and N in both laboratory bioassays and *in situ* field experiments (e.g. Ahern *et al.* 2008a; Ahern *et al.* 2007a), strengthen the importance of rating areas high in
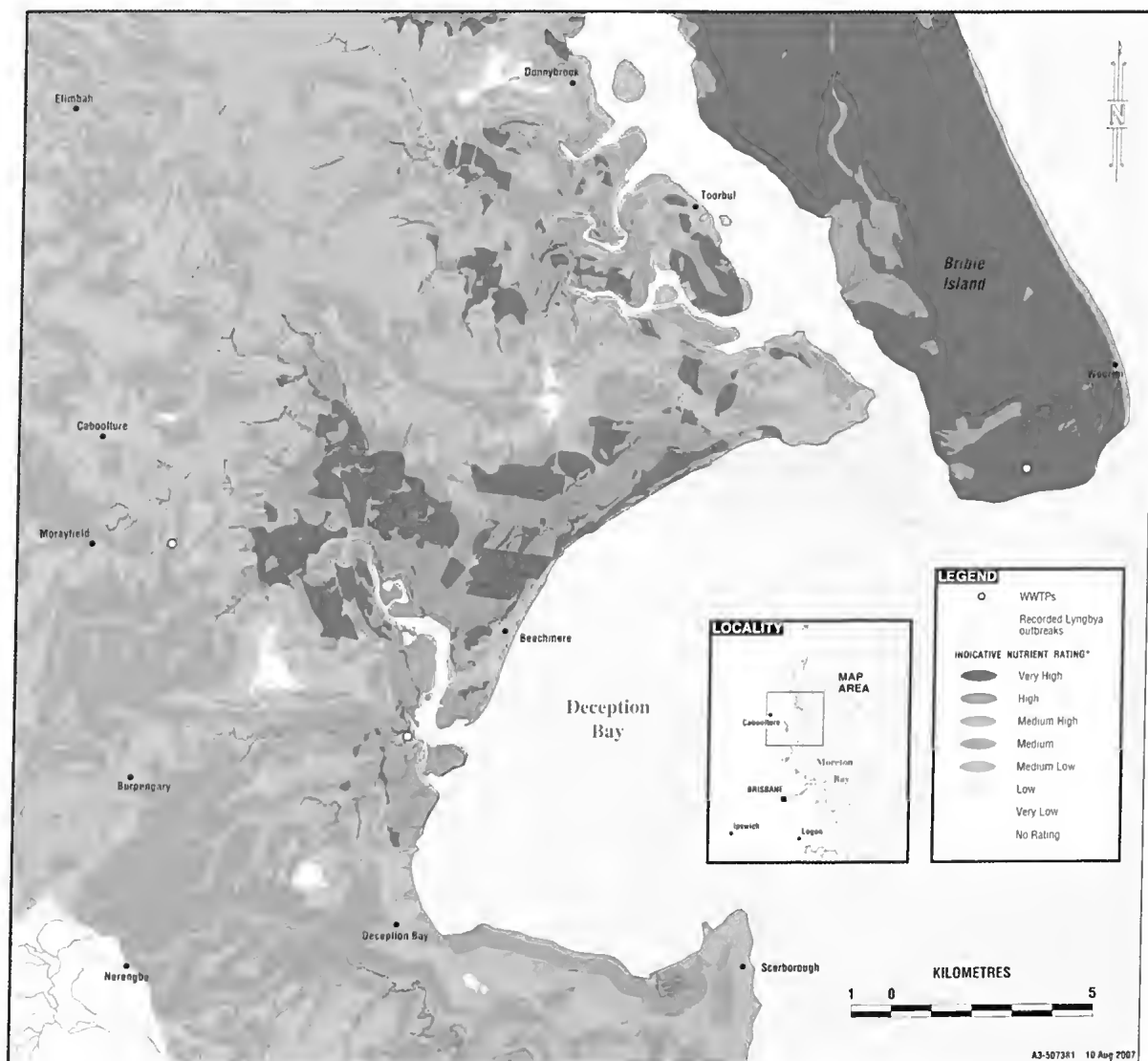
FIG. 3. Meso-scale nutrient hazard map of the Deception Bay and southern Pumicestone Passage area.

these nutrients as a hazard. Ahern *et al.* (2008b, this volume) also shows Fe, organics or P in groundwaters from these areas to be appreciable. Therefore, we added a high rating to areas of pine plantations, *Melaleuca* and ASS, not already rated high or very high in Figure 3, and produced a nutrient hazard map (Fig. 4) for use by planners and managers to assist decision making.

MACRO-SCALE MAP

The macro-scale map (Fig. 5) indicates those areas most vulnerable to the supply and delivery of relevant nutrients to the coast, are the sand islands of Moreton Bay, the horticulture, agriculture and ASS areas of the Logan, Caboolture, Maroochy and Mooloolaba Rivers, and the pine plantation areas adjacent to Pumicestone Passage. The methods used in the modelling process provide a means of combining the information from all the different layers, giving a cumulative nutrient hazard rating.

LIMITATIONS OF GIS AND MODELLING APPROACH

In developing the model, some challenging issues were encountered with GIS coverages
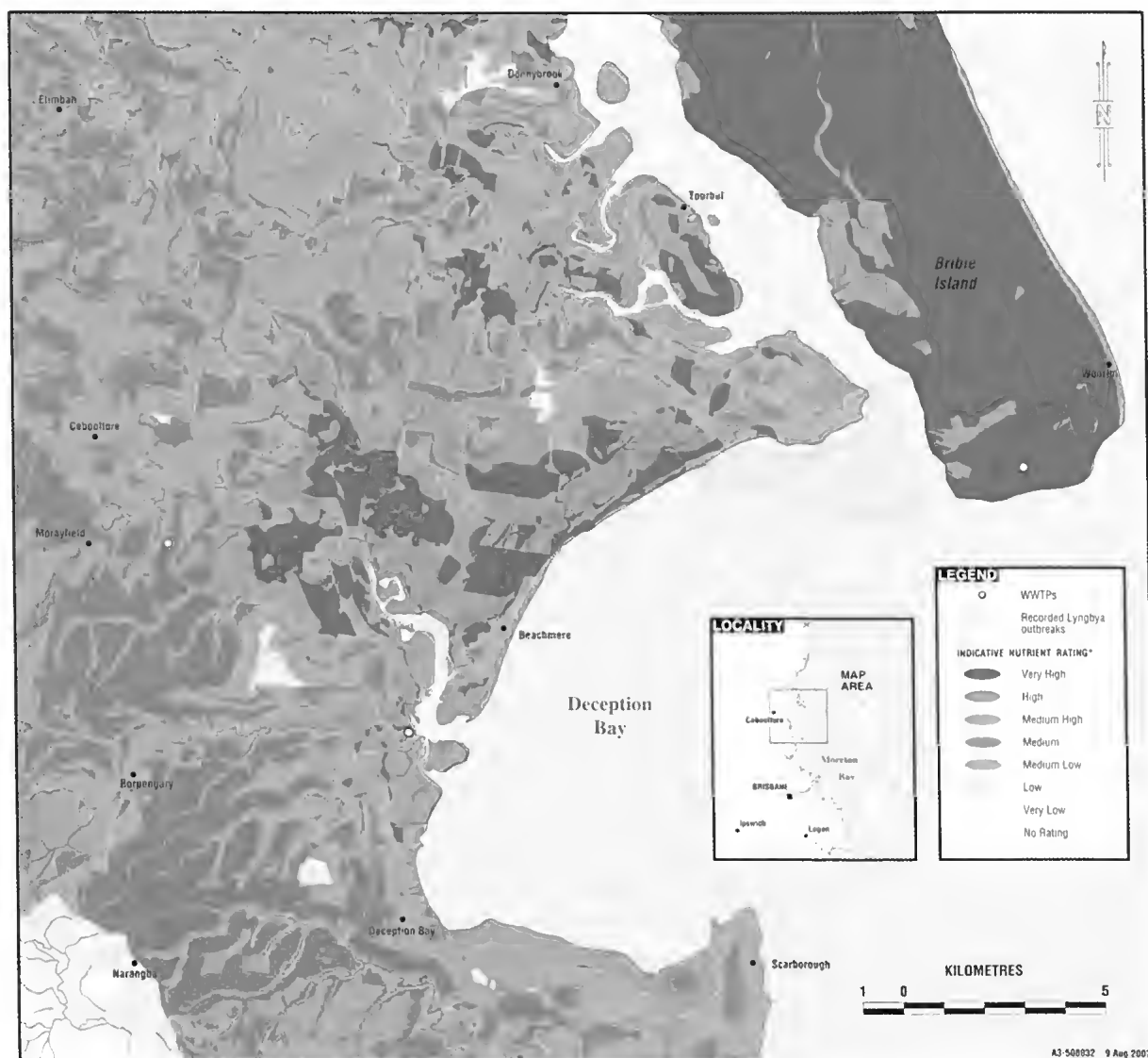
FIG. 4. Meso-scale nutrient hazard map of the Deception Bay and southern Pumicestone Passage area including the addition of pine plantations, Melaleuca, and ASS.

such as different map scales (1:25 000 to 1:2 000 000 for soils), different coastal boundaries and different methods of mapping. For example, vegetation coverages extend beyond highest astronomical tide (HAT) to low water mark where mangroves and other salt tolerant vegetation grow, while landuse and soil coverages commonly use high tide mark or HAT. Differences in scale, or gaps in coverages, can also be an issue. The eastern edge of Bribie Island, and the southern Deception Bay area of Rothwell and Kippa-Ring, display some of these GIS issues (Fig. 3).

The final model represents the combined impact of all factors likely to influence nutrient export from land sources. A limitation with the spatial method of representation is that it cannot easily represent the relative importance of major nutrient point sources (e.g. sewage treatment plants) due to their small spatial extent. Also, there is no represention of areas using septic systems rather than reticulated sewage. This would be a useful addition to future projects, as septic systems supply considerable amounts of labile nutrients to the groundwater
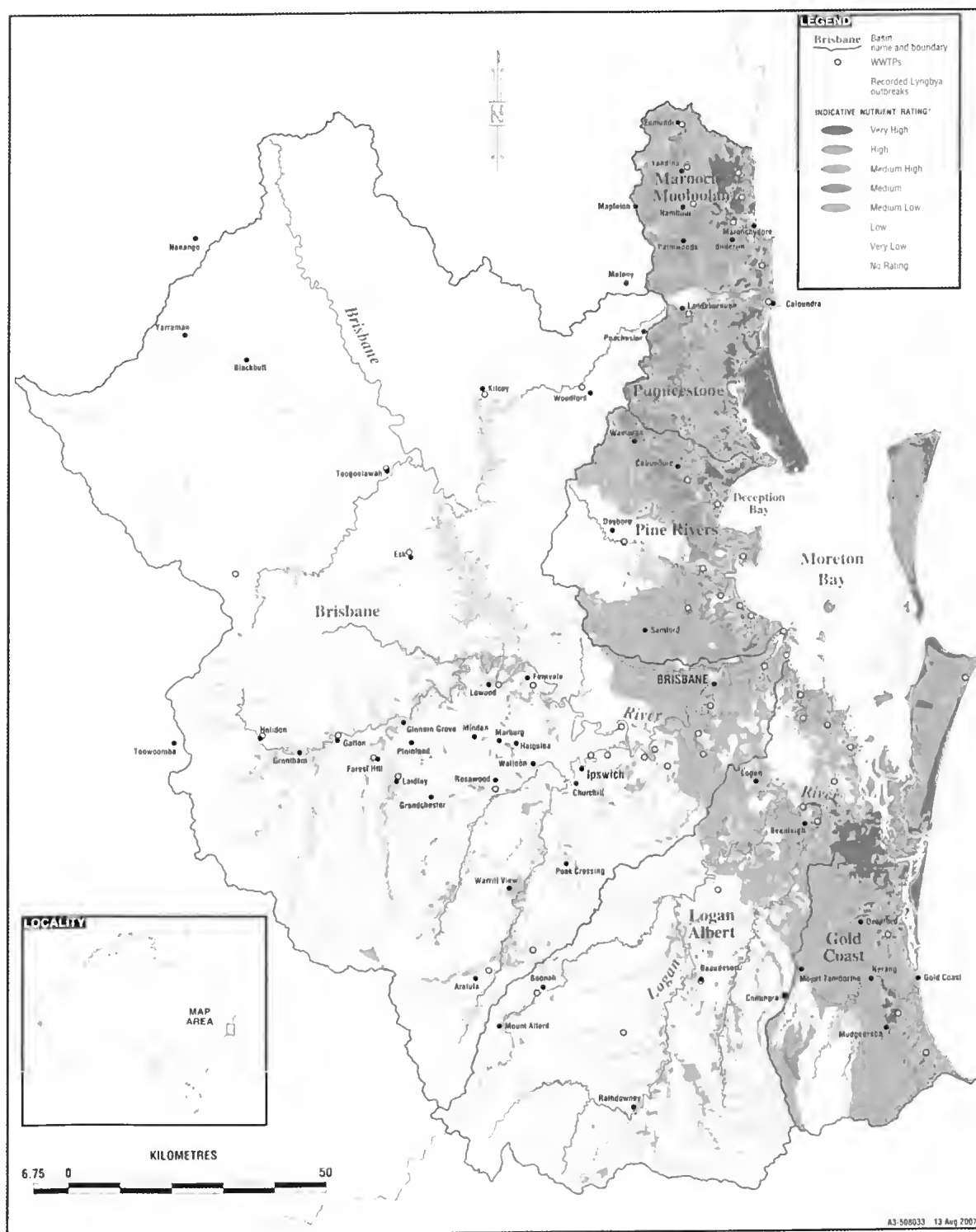
FIG. 5. Macro-scale indicative nutrient hazard map of Southeast Queensland including the addition of pine plantations, *Melaleuca*, and ASS.

(Whitehead *et al.* 2003). Finally, a model is only as good as its data sources, and so it is highly recommended that the 1999 land use coverage be updated to reflect the many land use changes that have since taken place in southeast Queensland.

A major benefit of this technique is that the model can be re-run, and new maps produced, as new information and updated coverages become available. Within the model, heavy emphasis has been placed on the transport mechanism ('coastal and stream proximity' layer), since it is only when the nutrients reach the shallow coastal and estuarine waters of Moreton Bay that they can contribute to the growth of *L. majuscula*. The results of this emphasis can be seen in the meso-scale map (Fig. 4), where areas >1km from streams have a lower rating.

Information being gathered regarding *L. majuscula* growth factors has been used in Bayesian modeling (Hamilton *et al.* 2005). Future developments will be to combine or replace the proximity coverage with sediment and nutrient run-off models such as E2 (eWater Cooperative Research Centre, Canberra). Such a project is under consideration for future funding.

CONCLUSION

Southeast Queensland's fast growing population is forcing significant land use changes. Resultant disturbance and changes to drainage patterns will continue to affect the supply and delivery of nutrients to the waters of Moreton Bay. The model and resulting maps from this investigation provide an assessment as to where to concentrate efforts to limit or reduce the 'nutrients of concern' that contribute to blooms of *L. majuscula*.

Maps from the earlier version of the model were incorporated as tools into the *Algal Blooms* policy 2.4.7 in the *Southeast Queensland Regional Coastal Management Plan* (EPA 2006). Subsequent research and further soil sampling continue to support the findings displayed in the original maps. Fine tuning of the model has resulted in new nutrient hazard maps (Figs 4, 5), and although similar to the early versions, these new maps provide an update.

Appropriate nutrient management guidelines need to be developed for industry use when disturbing areas rated high or very high in the nutrient hazard maps.

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Ecophysiological status of nine species of macroalgae and seagrasses in Moreton Bay, Queensland, Australia

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ABSTRACT

Macroalgae and seagrasses from subtropical Moreton Bay on the east Australian coast were measured *in situ* using a submersible pulse-amplitude modulated fluorometer (Diving-PAM). The measurements from these marine phototrophs growing in the relatively pristine waters of eastern Moreton Bay will provide useful baseline information for future comparable studies assessing anthropogenic-induced environmental stresses, like those that now exist in the western part of the Bay. Importantly, this study redresses the paucity of knowledge on macroalgae that currently exists in this region. The use of this chlorophyll-fluorescence technique was attractive because of its non-invasive, quantitative approach providing information on photosynthetic performance of both macroalgae and seagrasses without the need for transplanting or enclosures. ❑ *ecophysiology, photosynthesis, phototrophs, chlorophyll, fluorescence, seagrass, macroalgae*

Macroalgal and seagrass beds rank among the most productive communities in the biosphere (Mann 1973; Ziemann & Wetzel 1980; Charpy-Rouband & Sournia 1990; Duarte & Chiscano 1999). They maintain a number of ecosystem functions, such as providing carbon and nutrient (N and P) sinks, food and habitat for animals, oxygenation of the water column, and consolidation of marine sediments. These marine phototrophs act as an interface between the water column and the sediments, extending metabolically active surfaces into the water column (leaves and fronds) and into sediments and other marine substrata (holdfasts, stolons and roots). Pristine marine systems are usually characterised by species rich macroalgal communities and extensive seagrass beds (Shepherd *et al.* 1989; Duarte 1995; Eriksson *et al.* 1998). As such they are useful biological indicators of disturbance which is frequently a consequence of human activity.

The macroalgal and seagrass communities of Moreton Bay (Fig. 1) reflect the markedly different environmental conditions prevailing in the western and eastern sectors of the bay (Young & Kirkman 1975; Hyland *et al.* 1989). Western Moreton Bay is heavily impacted by suspended solids, high nutrient loads and low salinity water from sewage discharge, terrestrial and riverine runoff. Consequently, the seagrass communities along the mainland coast of the bay are both sparse and largely restricted to
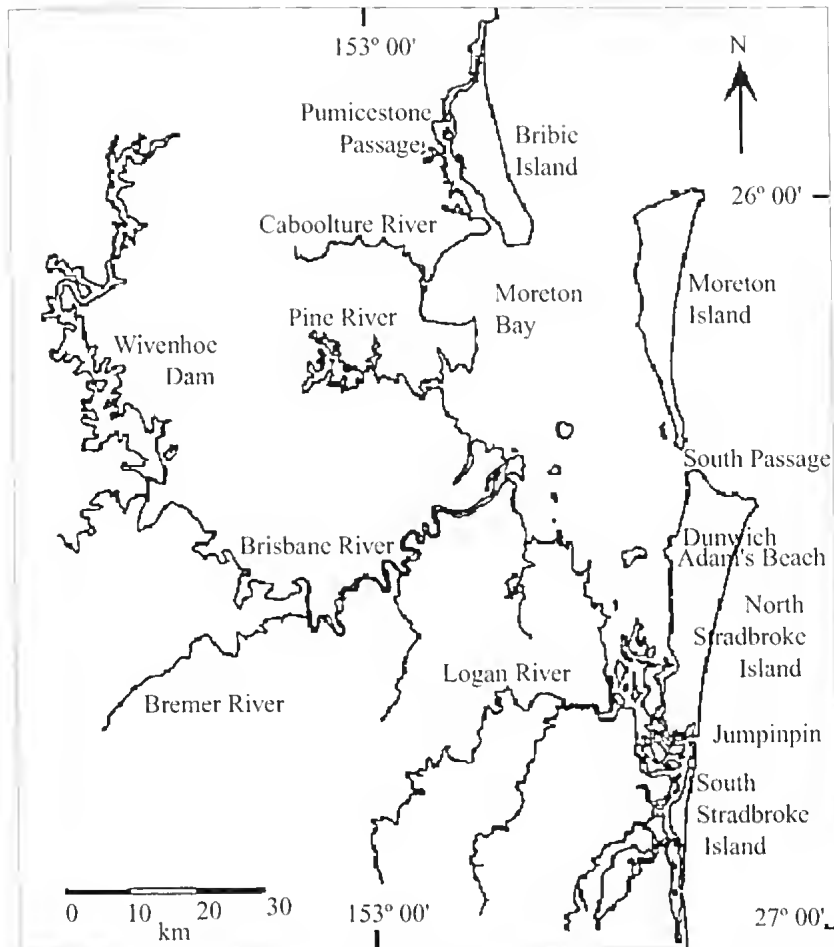
FIG. 1. Moreton Bay region of Southeast Queensland, Australia. Sampling sites were at Dunwich and Adam's Beaches on North Stradbroke Island.

depths <3 m. Macroalgal and cyanobacterial blooms, particularly of *Ulva* spp. and *Lyngbya majuscula*, are common in western Moreton Bay (Phillips pers. obs.). Increased nutrient loading favours the growth of opportunistic, stress-tolerant, bloom-forming macroalgal species that out-compete slower growing macroalgal and seagrass species for space and resources (Brown *et al.* 1990; Duarte 1995; Morand & Briand 1996; Hernandez *et al.* 1997; Raffaelli *et al.* 1998; McGlathery 2001; Taylor *et al.* 2001). Eastern Moreton Bay, on the other hand, undergoes constant flushing with oligotrophic oceanic waters. This relatively pristine environment supports dense and extensive seagrass meadows on the sandy substrata (Young & Kirkman 1975; Hyland *et al.* 1989).

In this study, chlorophyll fluorescence measurements were used to assess the physiological status of selected species of macroalgae and seagrasses growing in the relatively pristine waters of Eastern Moreton Bay (Fig. 1). The *in situ* photosynthetic capacity of these species (Table 1) was measured using a submersible pulse-amplitude modulated (PAM) fluorometer (Diving PAM). This measures efficiency of photochemistry from the fluorescence signal emitted by the phototrophs. The technique is non-destructive, rapid and adaptable to a range of aquatic photosynthetic organisms including benthic microalgae, seagrasses, macroalgae and corals. It is also a very sensitive indicator of perturbations in the photosynthetic process that may be due to changes in environmental

factors (Maxwell & Johnson 2000). The interpretation of the findings however, must be treated with care particularly when working with field samples that have an unknown nutrient history (Kruskopf & Flynn 2006; Raven & Beardall 2006). The quantum yield of photochemistry measured with PAM fluorometers has been used as a sensitive indicator of photosynthetic stress in seagrasses (Ralph 1999). Ralph & Burchett (1995) reported that fluorescence was more sensitive than oxygen electrode techniques for monitoring irradiance stress. PAM fluorescence has also been used to measure salinity stress (Kamermans *et al.* 1999), and carbon limitation (Schwarz *et al.* 2000) in seagrasses. Given these applications, measuring the photosynthetic health of marine phototrophs, growing in the clean waters of Eastern Moreton Bay, will provide valuable baseline information for future studies assessing anthropogenic induced stresses such as elevated nutrient levels, toxicants, turbidity effects and altered salinity levels that now exist in Western Moreton Bay.

MATERIALS AND METHODS

STUDY SITE

Moreton Bay (27°S, 153°E) is an important subtropical estuary in Southeast Queensland, Australia (Fig. 1). It is approximately 1400 km² with a maximum depth of 40 m in the north and 6 m in the south. Located adjacent to the City of Brisbane, the bay is separated from the South Pacific Ocean by Moreton, North and South Stradbroke Islands. Terrestrial runoff into the western side of the bay comes largely from four river catchments: Logan, Brisbane, Pine, and Caboolture (Fig. 1) while water exchange with the ocean (eastern side) occurs via the wide northern opening, between Bribie and Moreton Islands, South Passage situated between Moreton Island and North Stradbroke Island to the east, and Jumpinpin to the south. The study sites were located on the west coast of North Stradbroke Island (Fig. 1).

SAMPLE COLLECTION

Macroalgae and seagrasses (Table 1) were examined, *in situ*, at low tide (0–1 m) between 800 and 1100 hrs at Adam's and Dunwich Beaches on the eastern side of Moreton Bay (Fig. 1) during the period 7–25 February 2005 as part of the Thirteenth International Marine Biological Workshop on the Marine Fauna and Flora of Moreton Bay. These are soft sandy beaches with extensive macroalgal and seagrass communities. Plants were assessed immediately on site using a Diving-PAM (Pulse Amplitude Modulated) fluorometer (Walz, Germany) as described below. The green macroalgal species *Codium platyclados* and *Codium spongiosum* and the seagrass *Syringodium isoetifolium* were

Table 1. List of marine plants investigated and their geographical distributions. Abbreviated code names (four letters) were used to label figures.

Plant	Higher Taxon	Code	Distribution
Macroalgae			
Caulerpa taxifolia (Vahl) C.Agardh	Chlorophyceae	C tax	pan tropical/subtropical
Codium platyclados R. Jones & Kraft	Chlorophyceae	C pla	east coast Australia
Codium spongiosum Harvey	Chlorophyceae	C spo	tropical Indopacific
Padina australis Hauck	Phaeophyceae	P aus	pan tropical/subtropical
Padina gymnospora (Kuetzing) Sonder	Phaeophyceae	P gym	pan tropical/subtropical
Seagrasses			
Zostera capricorni Ascherson	Zosteraceae	Z cap	endemic
Cymodocea serrulata (R. Brown) Ascherson & Magnus	Cymodoceaceae	C ser	tropical Indopacific
Halophila ovalis (R. Brown) Hooker f.	Hydrocharitaceae	H ova	pan tropical/subtropical
Syringodium isoetifolium Ascherson Dandy	Cymodoceaceae	S iso	tropical Indopacific

Table 2. List of parameters used, their abbreviations and units. Fluorescence definitions and equations were taken from Maxwell & Johnson (2000).

Parameter	Definition and equation	Units
PAM	pulse amplitude modulated fluorometer	
PAR	photosynthetically active radiation	μmol photons m^{-2} s^{-1}
PSII	photosystem two	
F	background fluorescence	relative units
F_o	minimal fluorescence yield (in dark); all PSII reaction centres are open while the photosynthetic membrane is in the non-energised state; i. e., $q_P = 1$ and $q_N = 0$	relative units
F_m	maximum fluorescence yield (in dark); all PSII reaction centres are closed; all nonphotochemical quenching processes are at a minimum; i. e., $q_N = 0$	relative units
F_o'	minimum fluorescence yield subsequent to exposure to actinic and far-red light; all PSII reaction centres open in any light adapted state; i. e., $q_P = 1$ and nonphotochemical quenching ≥ 0	relative units
F_m'	maximum fluorescence yield (in light) obtained by a saturation pulse during exposure to actinic light; all PSII reaction centres closed in any light adapted state; i. e., $q_P = 0$ and nonphotochemical quenching ≥ 0	relative units
$\Delta F / F_m'$	effective quantum yield of photosynthetic energy conversion; Genty parameter. $= (F_m' - F_o') / F_m'$	relative units
qP	photochemical quenching coefficient; varies between 0 and 1. $= (F_m' - F)/(F_m' - F_o)$	relative units
NPQ	nonradiative energy dissipation; varies between 0 and 10. $= (F_m - F_m')/F_m'$	relative units
Rel. ETR	relative electron transport rate of PSII $= \Delta F/F'_m \times PAR \times 0.5 \times AF$	μmol electrons m^{-2} s^{-1}
AF	absorptance factor; 0.84	relative units

collected from both Adam's and Dunwich Beaches. As there were no significant differences in fluorescence responses between locations, we grouped the data for each species.

PHYSICAL AND CHEMICAL PARAMETERS

Water quality parameters (salinity, pH and temperature) at collection sites were measured in the field using a Horiba Water Quality Checker (Model U-10, California, USA). Dissolved O_2 was measured with an YSI Environmental Oxygen Probe (John Morris Scientific Pty Ltd).

FLUORESCENCE MEASUREMENTS

We assessed the photosynthetic activity in a variety of macroalgae and seagrasses from Moreton Bay by measuring chlorophyll fluores-cence signals from photosystem II (PSII) with a Diving-PAM (Walz, Germany). Fluorescence measurements were recorded from at least 2–3 separate blades/leaves from a minimum of three discrete plants of each species. *In situ* measurements were made on the actively-growing parts of the plant by positioning a fibreoptic-measuring head 10 mm from the plant tissue. To avoid effects associated with dessiccation and elevated temperature, the leaf/blade was kept immersed in seawater at its collection site and assayed within minutes of harvesting. The same measuring intensity and gain settings were used for all measurements and we were careful not to shade the plants being measured. Table 2 lists all fluorescence

parameters measured, their definitions, equations and units.

The Diving PAM allowed us to meaure fluorescence in ambient daylight and collect information on quenching coefficients. The effective quantum yield of photosynthetic energy conversion ($\Delta F / F'_m$) was calculated according to the relationship $(F'_m - F)/F'_m$ where F'_m is the maximum fluorescence yield of an illuminated sample and F is the background fluorescence for a given light state before a saturating light pulse. $\Delta F / F'_m$ is also referred to as the Yield or Genty-parameter (Genty *et al.* 1989).

Photosynthetic activity was estimated from the apparent relative electron transport rate of PSII (rel. ETR) which was determined using the relationship of Genty *et al.* (1989): relative ETR (μmol electrons m^{-2} s^{-1}) = quantum yield ($\Delta F / F'_m$) × PAR × 0.5 × absorptance factor (AF). The PAR value is the instantaneous photosynthetic active irradiance (μmol photons m^{-2} s^{-1}) directly measured close to the sample by the Diving PAM quantum sensor. The constant, 0.5, corrects for the fact that two quanta of light are required per electron as there are two coupled photosystems simultaneously absorbing light. The factor of 0.5 comes from the assumption (not always correct) that half the absorbed photons are used by PSII and half by photosystem I (PS I). The absorptance factor defines the fraction of incident light absorbed by the phototroph. As a best approximation we used the average light absorptance value of terrestial plant leaves AF = 0.84 (Björkman & Demmig 1987). There is however, a three-fold range of absorptances within seaweeds as a function of genotype and PAR environment (Table 4; Lüning 1990).

Table 3. Water quality parameters measured, between 8:00 and 11:00 hrs, at Adam's and Dunwich beaches during the study period. These parameters varied by less than 10% between sampling sites so the ranges over collection dates has been presented.

Parameter	Range
Salinity (ppt)	32–38
pH (rel units)	7.7–8.0
Water temperature (°C)	25–29
Dissolved O_2 (mg. L^{-1})	5.4–6.4
O_2 saturation (%)	82–96

The fluorescence quenching coefficients calculated by the instrument's subroutine program include photochemical quenching (qP) and nonradiative energy dissipation (NPQ), a type of nonphotochemical quenching. Photochemical quenching gives an indication of the proportion of PSII reaction centres that are open (photochemistry saturated) on a scale of zero to one. NPQ reflects heat-dissipation of excitation energy in the PSII antenna system so that it is a convenient indicator of excess light energy. The expression of nonphotochemical quenching (NPQ) used by the Diving PAM (Table 2) is based on the matrix model of antenna organisation and assumes the existence of nonphotochemical quenching traps (Schreiber *et al.* 1994). The sum of all the quenching processes is constant over wide variations in irradiance, indicating that they may be actively involved in the regulation and control of dissipation and utilisation of excitation energy in response to the current requirements of the photosynthetic apparatus (Maxwell & Johnson 2000).

RESULTS

Water quality parameters did not vary significantly between collection sites and collection dates (Table 3). Water temperature (27 ± 2°C), salinity (35 ± 3 ppt) and pH 7.85 (± 0.15 pH units) were typical for these sites at this time of the year. The water column was homogenously oxygenated with dissolved O_2 concentrations in the range 5.4–6.4 mg. L^{-1} (Table 3).

In situ chlorophyll *a* fluorescence measurements revealed a range of photosynthetic activity amongst the macroalgal and seagrass species examined (Figs 2-5). Yield values ranged from 0.48 ±0.09 for the seagrass *Cymodocea serrulata* to 0.85 ±0.05 for the brown alga *Padina gymnospora* (Fig. 2). The average $\Delta F / F_m'$ value for all plants measured in the present study was 0.72 ±0.06. This is similar to the Yield value typically reported in the literature for macroalgae and seagrasses from around the world (Table 4).

In general, macroalgae had lower rel. ETR values than the seagrasses (Fig. 3). The green algae, *Caulerpa taxifolia, Codium platyclados* and

Table 4. Literature values for various photosynthetic parameters measured with PAM fluorometers on seagrasses and **macroalgae**. In cases where parameters were measured but not reported, we used 'nr' to indicate 'not reported'. **Y** = Quantum yields; **Fv/Fm** = Photo-synthetic efficiency; **AF** = Measured absorption factor; **rel. ETR** = relative electron transport rate. Literature values for rel. ETR were calculated as described above in the methods section in most papers (§). However, some calculated rel. ETR without including AF (#) while others did not use AF or 0.5 (^).When errors were given as plus or minus standard deviations, we included them.

Species	Location	Y	Fv/Fm	AF	rel. ETR	Comments	Reference
terrestrial plant leaves			0.83	0.84			Björkman & Demmig (1987)
Zostera marina Cymodocea nodosa				0.44 ± 0.02 0.72			Beer et al. (1998)
Posidonia australis P. sinuosa Amphibolis antartica A. griffithii Halophila ovalis	Rottnest Island, Australia		ave = 0.68 ave = 0.70 ave = 0.63 ave = 0.55 ave = 0.58	0.84 §	max. 48 max. 27 max. 22 max. 30 max. 52	sampled between 5:00-19:00 hrs	Ralph et al. (1998)
Thalassia testudinum	Puerto Morelos, Mexico	nr	0.81	0.69	230	start of experiment (control)	Enríquez et al. (2001)
Ulva lactuca	Coobowie Australia	0.70-0.45		0.50	10 - 50	sampled between 900 & 1600 hrs	Longstaff et al. (2004)
Thalassia testudinum	Florida Bay, USA	0.78 ± 0.02	0.78 ± 0.03	0.67 ± 0.03	nr	youngest leaf measured	Durako & Kunzelman (2002)
Zostera marina	Chesapeake Bay, USA		0.75 - 0.80		20 - 45 ^	range given	Ralph et al. (2002)
Laminaria saccharina	Northern Brittany, France	0.15-0.73	0.74 ± 0.01		19 - 49 #	sampled between 1100 & 1800 hrs	Gévaert et al. (2003)
Posidonia australis	Jervis Bay, Australia	0.70 ± 0.06		0.68 ± 0.16	47 - 65	mean values	Runcie & Durako (2004)
Halimeda tuna	Florida Keys, USA				10 - 20	range given	Smith et al. (2004)
Thalassia hemprichii	Wanlitung, Taiwan			0.84 §	219 ± 20	sampled between 1000 & 1600 hrs	Liu et al. (2005)

Codium spongiosum had an average rel. ETR of 7.38 ±2.55 μmol electrons m⁻² s⁻¹ which was not significantly different to that measured for the brown algae *Padina australis* and *Padina gymnospora* (7.43 ±1 μmol electrons m⁻² s⁻¹) (Fig. 3). While there is little overall variation in photosynthetic efficiency between the macroalgal genera, there is a great deal of variation between macroalgae and seagrasses (Fig. 3). On average, rel. ETR for the four seagrasses examined was 22 ±3 μmol electrons m⁻² s⁻¹ (Fig. 3), about three times that measured for the macroalgae. The two seagrasses, *Halophila ovalis* and *Syringodium isoetifolium* were the most productive of all the plants measured (rel. ETR > 32 μmol electrons m⁻² s⁻¹; Fig. 3). Given that rel. ETR values can be used as a proxy for photosynthetic activity (gross), our findings (Fig. 3) reveal that the seagrasses in Moreton Bay are more productive (gross) than macroalgae.

Eighty percent of the PSII reaction centres in the plants (Fig. 4) were open at the time of measurement as indicated by the average qP for nine marine plants (0.8 ±0.09). All plants have qP values of 0.76 with the exception of *Cymodocea serrulata* which had a qP of 0.48. This seagrass also had a relatively low Yield of 0.48 (Fig. 2). The average NPQ for macroalgae (4.61) was similar to that for seagrasses (4.96) (Fig. 5). NPQ varied from 2.67 for *Padina australis* (Phaeophyta) to 8.41 for *Padina gymnospora* (Fig. 5). There were no evident trends in NPQ values between genera, taxa or families.

DISCUSSION

The measured fluorescence parameters provide a physiological summary of the photosynthetic performance of the nine marine plants examined under ambient environmental conditions. The phototrophs examined could be considered physiologically healthy based on their overall high Yields (Fig. 2), rel. ETR (Fig. 3), qP (Fig. 4) and NPQ (Fig. 5). Our findings for Yield and rel. ETR values are similar to those previously reported for plants growing in clean environments (Table 4). A photosystem's ability/efficiency to use light, expressed as rel. ETR, allows comparisons of photosynthetic efficiencies between different leaves and even between different plant species (Maxwell &

Johnson 2000; Beer *et al.*, 1998). Kevekordes *et al.* (2006) found that rel. ETR values varied 2-fold between eight species of *Caulerpa* ranging from 7–13 μmol electrons m⁻² s⁻¹. Interestingly, the broad form of the pan-tropical/subtropical green alga *Caulerpa taxifolia* (Phillips & Price 2002) we examined had an average rel. ETR of 7.3 μmol electrons m⁻² s⁻¹ (Fig. 3). Changes in environmental conditions such as anthropogenic inputs (e.g. nutrients, toxicants, suspended solids) adversely affect the photosynthetic process. These impacts are detected by lowered reaction rates of the primary light reactions, thylakoid electron transport, darkenzymic stroma reactions and/or slow regulatory feedback processes to name a few. Yield and rel. ETR values, recorded for the phototrophs in this study, are indicative of a healthy environment.

The two most productive seagrasses (Fig. 3), *Halophila ovalis* and *Syringodium isoetifolium*, have leaf morphologies atypical for seagrasses resulting in lower overall leaf area. Leaves of *Halophila ovalis* are 1–4 cm long and petiolate, with laminae 0.5–2 cm in breadth while the narrow cylindrical leaves of *Syringodium isoetifolium* are 7–30 cm long and <2 mm wide. In eastern Moreton Bay, these species typically occur in either intertidal environments to depths of 5 m (*Halophila ovalis*) or just below low tide mark (*Syringodium isoetifolium*) where they still receive ample light for photosynthesis due to high water clarity (Young & Kirkman 1975). High rel. ETR (Fig. 3) with high photochemical activity (Fig. 2) have previously been reported for *Halophila ovalis* (Ralph *et al.* 1999), considered a colonising species. On the other hand, *Zostera capricorni* and *Cymodocea serrulata*, with more typical leaf morphology for seagrasses, had the lowest rel. ETR values (Fig. 3). These grow in either the intertidal zone to depths of 8 m (*Zostera capricorni*) or subtidally to depths of 3 m (*Cymodocea serrulata*) (Young and Kirkman 1975). These species have strap-like linear leaves which are 7–50 cm long and 2–5 mm broad (*Zostera capricorni*) or 6–15 cm long and 4–9 mm broad (*Cymodocea serrulata*) maximising absorption of more photosynthetically active radiation. Previous studies (summarised in Table 4) have also found larger seagrasses generally have lower photosynthetic activity (Figs 2 and 3).
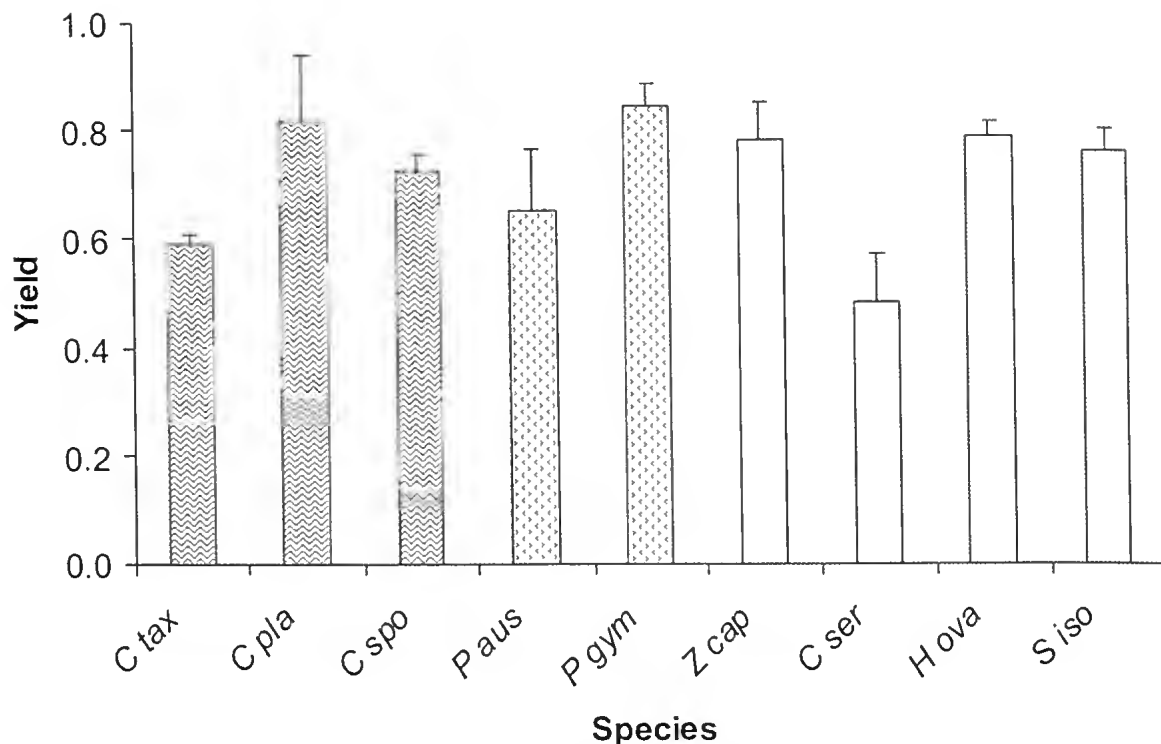
FIG. 2. Average Yield ($\Delta F/F_m$) ± SE for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined. High Yield values (>0.65) are an indicator of physiologically healthy plants. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

Unfortunately there are insufficient studies to make similar parallels for the macroalgae.

Diurnal rhythms of marine plants are known to influence *in situ* photosynthetic rate measurements. Beer & Björk (2000) observed that both F_v/F_m and rel. ETR decreased from early morning toward noontime in 2 seagrasses, *Halophila ovalis* and *Halodule wrightii*. Ralph *et al.* (1998) also observed significant diurnal variation in maximum ETR in three Australian seagrasses. Durako & Kunzelman (2002) found their Yield results were influenced by light intensity as well as by the selection of leaf tissue (age, health, etc.) and time of measurement. We endeavoured to make all our measurements on the actively growing sections of the marine plants and at approximately the same time of day (midmorning) to avoid these variables impacting on our results. While light intensity did vary with sampling time between 800 and 1100 hrs, we found no significant

relationship (p > 0.05) between Yield values, species and the light intensity at the time measurements were made. The statistically similar results obtained for the three phototrophs (*Codium platyclados, Codium spongiosum* and *Syringodium isoetifolium*) collected from different beaches on different days confirms we were successful in avoiding spurious results due to sampling protocols.

The rel. ETR values, presented, should only be used as a proxy for primary productivity. To calculate absolute photosynthetic ETR using PAM fluorometry, the AF for each plant and the incident irradiance at the point of the fluorescence measurement need to be determined (Beer *et al.* 1998). Unfortunately we were unable to measure the AF of the plants. Hence, for ETR calculations, we used the standard AF for leaves of higher plants (0.84; Björkman & Demmig 1987) to give rel. ETR values. This is the value built into the instruments subroutine.
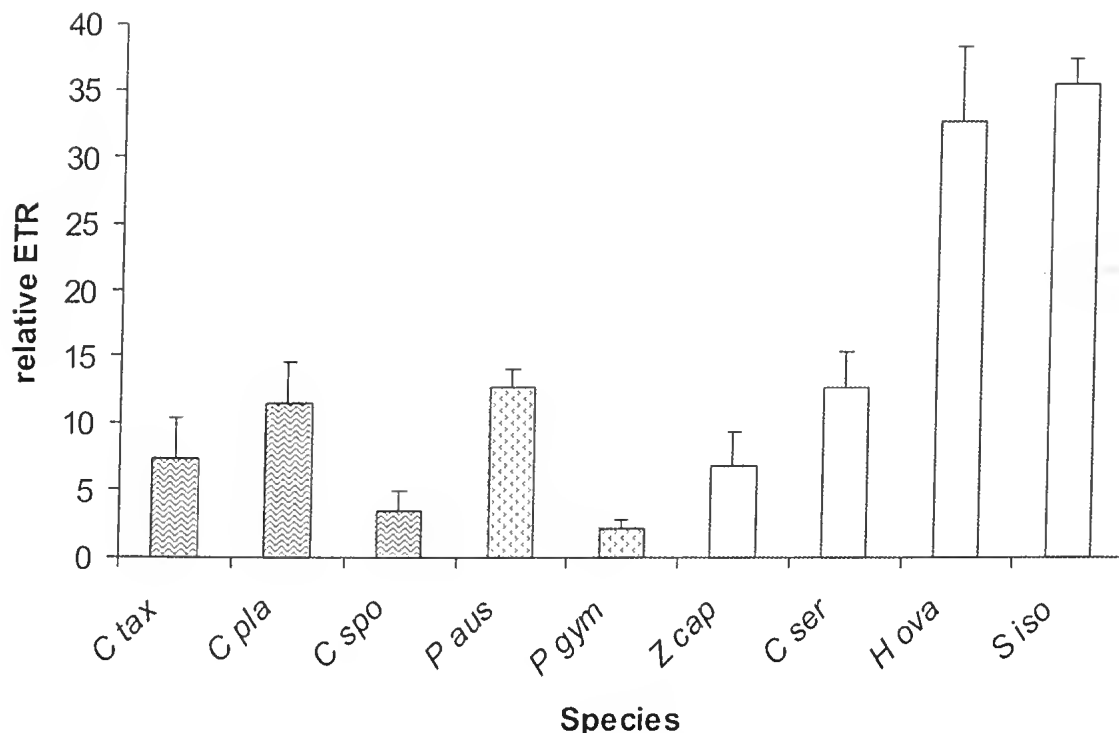
FIG. 3. Average rel. ETR (μmol electrons m^{-2} s^{-1}) ±SE for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined. The rel. electron transport rate can be used as a proxy for photosynthetic rate. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

A subsequent survey of the literature revealed AF values for macroalgae and seagrasses varies between 0.44 and 0.72 (Table 4). As these are all well below the AF for higher plants we have probably underestimated ETRs. Nonetheless, our rel. ETR were within the range of previously reported values when authors also used an AF of 0.84 (Table 4). Comparisons between plants and studies are reasonable as long as all the measuring parameters are clearly reported.

Assessment of overall photosynthetic performance has typically been made with the above parameters (Yield and rel. ETR) or their equivalents (F_v/F_m and primary productivity per unit of C or biomass). However, additional information on partial photochemical reactions can be obtained from analysis of induction kinetics which can reveal the complexity of the overall process. Saturation quench analysis, for example, allows us to distinguish between photochemical quenching coefficients. Fluorescence emission involves two fundamentally different types of competing de-excitation processes. First, photochemical energy conversion at the PSII centres and second, nonphotochemical loss of excitation energy at the antenna and reaction centre levels. Both mechanisms quench the maximal potential fluorescence yield according to the equations in Table 2. Because the Diving-PAM lacks an intrinsic far-red light source, the values presented here are only valid as first approximations.

An alternative expression for photochemical quenching (Table 2, Fig. 5) is 1-qP, the proportion of centres that are closed (Maxwell & Johnson 2000). This latter term is used as a measure of the excitation pressure on PSII. The macroalgae and seagrasses assessed in the present study had low amounts (0.2 ± 0.08) of excitation pressure on PSII (Fig. 4) indicating their photosynthetic apparatus coped with high photon fluxes which are typical of this region. Further, these measurements, along with the others undertaken in this study, show
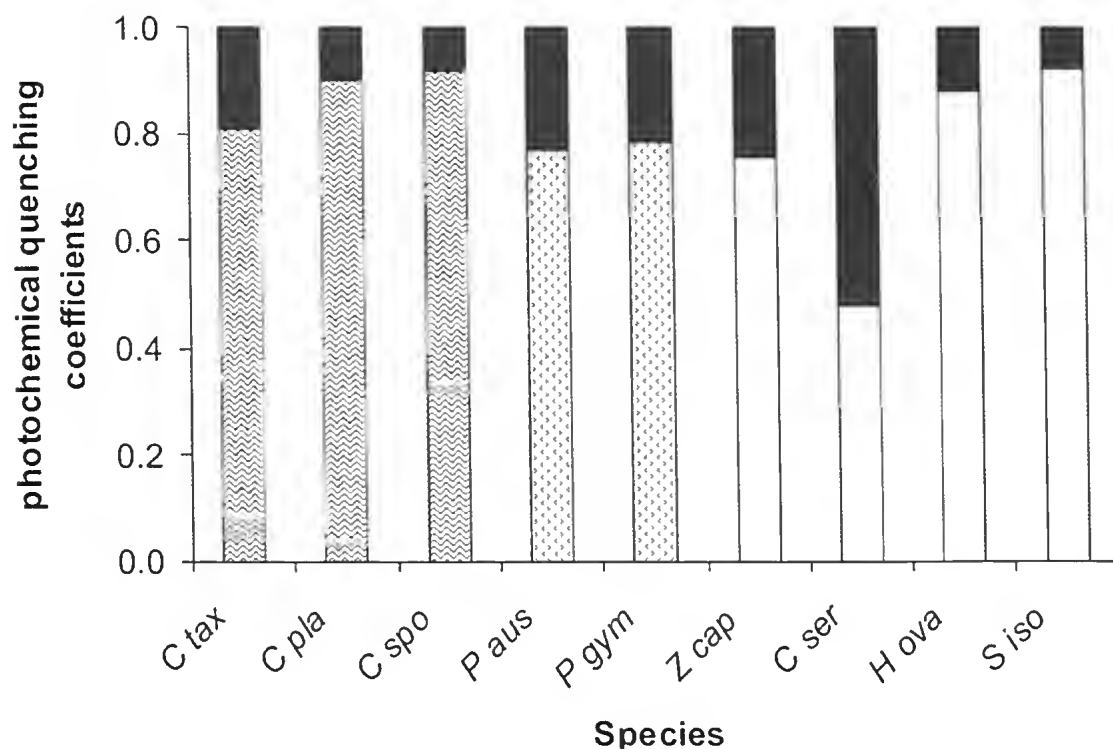
FIG. 4. The proportion of PSII reaction centres that are photochemically saturated (open) is defined on a scale of zero to one, and referred to as photochemical quenching (qP). On average, qP for macroalgal (shaded bars) and seagrasses (non shaded bars) was about 0.8. The average excitation pressure on PSII determined from the relationship 1-qP, was about 0.2 (filled bars for all species). Standard deviations were <20% of the means. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

that the plants were physiologically healthy. One exception was the seagrass *Cymodocea serrulata* which had a rather high 1-qP value of 0.52 (± 0.08) indicating that at least half of the open PSII reaction centres were suppressed by saturating light. This was consistent with the low Yield (Fig. 2) and rel. ETR (Fig. 3) measured for this species. There is no clear reason why this may be the case.

Non-photochemical quenching is due, in part, to heat-dissipation of excitation energy in the antenna system in the dark adapted state, or more simply, the amount of energy not used in photochemistry (Maxwell & Johnson 2000). Thus, NPQ is a useful indicator for 'excess light energy' and so is a good measure of photo-protection (Müller *et al.* 2001). Many of the macro-algae (the Chlorophyte *Codium platyclados*, the Phaeophyte *Padina gymnospora*) and the sea-grasses (*Cymodocea serrulata, Halophila ovalis*

and *Syringodium isoetifolium*) examined had high NPQ values (>4; Fig. 5). The remaining marine plants examined: *Caulerpa taxifolia* (Chlorophyta), *Codium spongiosum* (Chlorophyta), *Padina australis* (Phaeophyta) and *Zostera capricorni* (sea-grass) had NPQ values in the range typically associated with higher plants (0.5 and 3.5; Maxwell & Johnson 2000) (Fig. 5). All these NPQ values are consistent with the plants being well adapted to their respective light environments and with plants having high Yield values (average of 0.72) (Fig. 2) and qP values (Fig. 4). Marine plants, growing in their natural environment, appear to keep energy dissipation pathways always engaged and ready to protect. Plants exposed to high light intensities and frequent sunflecks generally maintain elevated levels of zeaxanthin, antheraxanthin, and xantho-phyll cycle pigments associated with photo-protective strategies (Demmig-Adams *et al.* 1999).
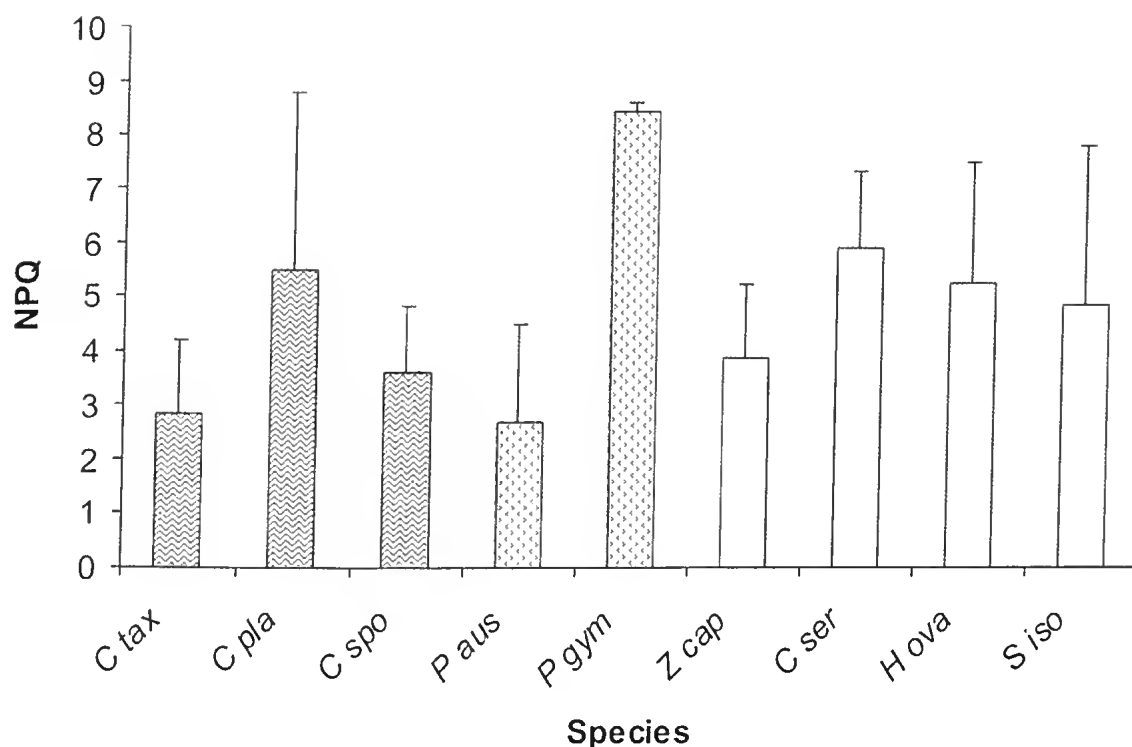
FIG. 5. Non photochemical quenching (NPQ) for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined . The error bars are standard deviations of n > 5 plants. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

Future studies should focus on examination of seagrasses and macroalgae in other parts of Moreton Bay, particularly those growing on the western mainland coast that are exposed to stresses such as reduced light penetration from increased water turbidity, reduced salinity from increased freshwater inflows from the river systems and increased nutrient loading from sewage and agricultural runoff as well as other source and non source point pollutants. Macroalgal and seagrass communities are important primary producers which underpin many food webs in Moreton Bay. Understanding the productivity, physiology and stress responses of these plants will provide useful management tools for the conservation of these species and the protection of the Moreton Bay ecosystem.

ACKNOWLEDGEMENTS

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An evaluation of the role of macroalgae in mangrove dieback at Whyte Island, Moreton Bay, subtropical eastern Australia

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ABSTRACT

The macroalgal/cyanobacterial assemblages of the Whyte Island mangal on the subtropical east Australian coast were investigated to determine if these assemblages had either contributed to, or had resulted from, mangrove dieback on the landward margin of the community. Habitat disturbance in the area is indicated by: lowered abundances of species of the red algal genera *Bostrychia*, *Caloglossa*, *Catenella* and *Murrayella*; the presence of green algal species under the mangal canopy; and a well developed microbial mat in the ponded area. None of these features are characteristic of healthy mangals in the Moreton Bay region. Impacts at Whyte Island from the ponding of water, discharge of sewage effluent, onshore algal blooms, and drifts from offshore blooms are discussed as possible causal factors for mangrove dieback. Algae and cyanobacteria respond quickly to environmental disturbance by showing a shift in species composition and abundance thereby providing a useful and much needed tool in assessing, understanding and dealing with perturbations in marine ecosystems. ❑ *mangrove dieback, tidal inundation, macroalgae, microbial mats, Microcoleus chthonoplastes*

Mangrove communities (mangals) typically occur on unconsolidated substrata (mud, sand, rubble) in the mid to high intertidal zone on sheltered tropical to warm temperate coasts worldwide (Chapman 1977; Hutchings & Saenger 1987; Saenger 2002). Only a relatively small number of terrestrial flowering plants have successfully colonised the harsh environment of the land/sea interface. Eighty-four species of mangroves (Saenger 2002) have evolved adaptations to overcome salt toxicity, physiological inaccessibility of water, anaerobic waterlogged soils and problems associated with dispersal and germination of reproductive propagules in the marine environment (Hutchings & Saenger 1987; Saenger 2002).

Mangals are amongst the most threatened ecological systems (Hutchings & Saenger 1987;

Hyland & Butler 1988; Field 1999; Bridgewater & Cresswell 1999; Alongi 2002; Saenger 2002). In the last 50 years, approximately one-third of the world's mangals have been destroyed by the activities of an ever increasing human population. Large areas of mangals have either been reduced to a degraded state or cleared for urban development, aquaculture and timber. Mangals are an invaluable ecological and economic asset, providing breeding and nursery habitats for a variety of animals including those contributing to the fishing industry, accumulation sites for nutrients and sediments, a renewable source of wood and protection against coastal erosion. Devising appropriate management strategies for these ecologically important ecosystems are crucial for both conservation and sustainable
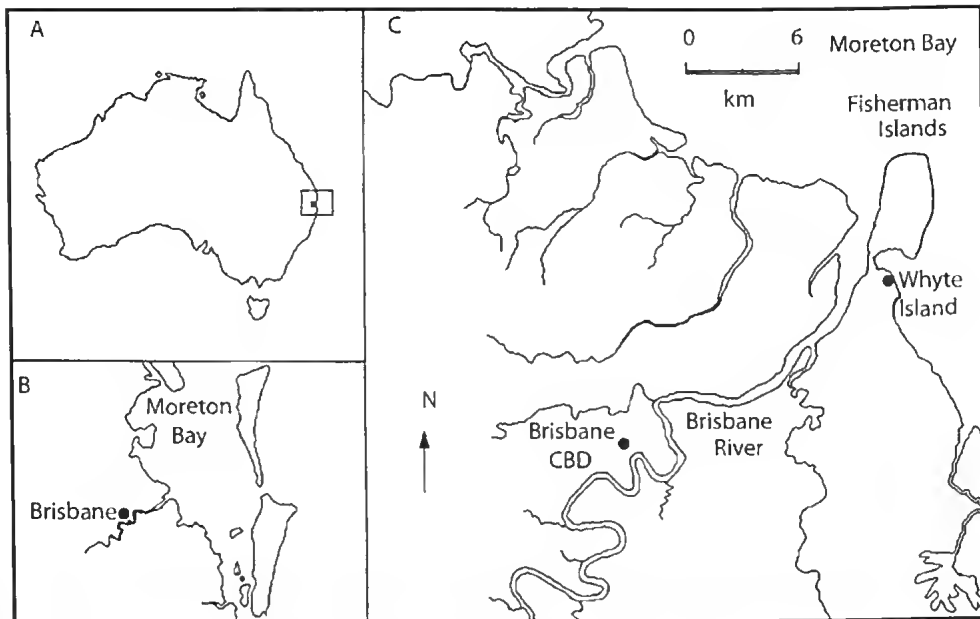
FIG. 1: Location of Whyte Island in Australia (A), the Moreton Bay region (B) and the mouth of the Brisbane River (C).

FIG. 2: Before the construction of Port Drive from 1972–1978, Whyte Island was surrounded by an extensive mangal. Crab Creek (white arrowheads) flowed from the Brisbane River between Whyte Island and the mainland coast and into Moreton Bay. The Wynnum North Sewage Treatment Plant (STP) discharged effluent via a sewer line into Crab Creek (black arrowhead).

use — the two key objectives of the Convention of Biological Diversity.

Seven species of mangroves occur in the extensive mangals on the sheltered shores of subtropical Moreton Bay, with three species being widely distributed. *Avicennia marina* is the most common and widespread species, growing along rivers and coastlines. *Rhizophora stylosa* occurs behind the *Avicennia marina* zone in the bay as well as in sheltered inlets and creeks. *Aegicerus corniculatum* is most common along the lower reaches of rivers and creeks (Dowling 1986; Hyland & Butler 1988).

Macroalgae are common components of healthy mangals, often growing on the trunks and aerial roots (pneumatophores, cone roots, stilt roots, knee roots, buttresses) of mangrove trees, and on any other firm substrata (rocks, mollusc shells, wood) on the mangal floor. Species of the red algal genera *Bostrychia*, *Caloglossa*, *Catenella* and *Murrayella* form the typical epiphytic algal com-

munity of mangals, commonly referred to as the *Bostrychia/ Caloglossa* association or the Bostrychietum (Post 1937; King & Puttock 1994; Phillips *et al.* 1994; Laursen & King 2000).

The macroalgae of Queensland mangals have been little studied. Cribb (1979) provided a general descriptive account of the macroalgae of Moreton Bay mangals. Atherton & Dyne (1977) collected quantitative data on macroalgal species along transects in the Serpentine Creek area, near the mouth of the Brisbane River. One of the authors (J.A.P.) has undertaken a systematic ecological survey along sea-to-land transects through a number of mangals in Moreton Bay to gather quantitative data on macroalgal species composition, abundance and distribution (Phillips, in prep.).

Considerable development along the mainland coast of Moreton Bay has caused the large scale loss of mangals either through direct removal of trees or indirectly from environmental disturb-

FIG. 3: Mangrove dieback at Whyte Island observed in September 2004. Crab Creek (yellow arrowheads) is truncated by Port Drive. The Wynnum North Sewage Treatment Plant (STP) discharges effluent via a sewer line (white arrowheads) and outfall (white arrow) into Crab Creek. The transect (black line) surveyed by the present study stretches from the seaward edge of the mangal to the smaller of the two dieback (D) areas.

ance. The progressive loss of mangal on Whyte Island near the mouth of the Brisbane River since the 1970s is a good example (Fig. 1). The island now has two large treeless areas between Port Drive and a narrowing seaward fringe of *Avicennia marina* (WBM 2002). This paper investi-

gates the species composition and abundance of macroalgal/cyanobacterial species inhabiting the Whyte Island mangal to determine if blooms or drifts of macroalgal/ cyanobacterial species are a consequence of, or have contributed to, the death of large numbers of *Avicennia marina* trees in the area.

MATERIALS AND METHODS

STUDY SITE

Prior to the 1970s, Whyte Island was largely covered by an *Avicennia marina / Rhizophora stylosa* mangal and separated from the mainland coast by Crab Creek (WBM 2002: Fig. 2). Between 1972 and 1978, a road (Port Drive) connecting Fisherman Islands to the mainland was constructed through the Whyte Island mangal and across Crab Creek which, together with subsequent industrial development to the west of the road, was responsible for the loss of 45 ha of mangal in the area. A large section of Crab Creek was infilled, leaving only a 50 m stretch of the creek to the east of Port Drive (WBM 2002). A sewer outfall discharges secondarily-treated effluent via a culvert directly into the remaining portions of Crab Creek.

Table 1. Survey of algal/cyanobacterial vegetation in the Whyte Island mangal on the 24th Feb 2005 and 19th July 2005. (+ = surveyed, – = not surveyed).

Quadrat No.	Distance from sea (m)	Feb. Survey	July Survey
1–3	0	–	+
4–6	15	+	+
7–9	40	–	+
10–12	80	+	+
13–15	140	–	+
16–18	145	+	+
19–21	145	–	+
22–24	150	+	+

Table 2. Survey of 24th Feb 2005.

Distance from Sea (m)	Quadrat No.	Pneumato-phore No.	% Canopy Cover	Low Tide Depth (cm)	Seedling No. (2–6 leaves)
Under mangrove canopy (15 m)	4	60	70	1	0
	5	80	80	2	0
	6	80	80	0	0
	Ave.	73.3	76.6	1	0
Under mangrove canopy (40 m)	7	50	70	1	5
	8	60	80	0.5	4
	9	35	70	1	4
	Ave.	48.3	73.3	0.8	5.3
Edge of dieback area (145m)	13	90	50	1	0
	14	80	60	1	0
	15	90	50	1	0
	Ave.	86.6	53.3	1	0
Dieback (ponded) area (150m)	19	8	0	5	0
	20	2	0	5	0
	21	1	0	5	0
	Ave.	3.67	0	5	0

Table 3. Survey of 19th July 2005.

Distance from Sea (m)	Quadrat No.	Pneumat-ophore No.	% Canopy Cover	Low Tide Depth (cm)	Seedling No. (2-6 leaves)
Sea edge (0m)	1	25	70–80	0	0
	2	40	70–80	0	0
	3	70	70–80	0	0
	Ave.	45	**70–80**	**0**	**0**
Under mangrove canopy (15m)	4	80	70–80	0	0
	5	80	70–80	0	0
	6	90	70–80	0	0
	Ave.	83.3	**70–80**	**0**	**0**
Under mangrove canopy (40m)	7	60	50	0	7
	8	80	60	0	6
	9	70	50	0	2
	Ave.	70	**53.3**	**0**	5
Under mangrove canopy (80m)	10	90	30	0	7
	11	60	50	0	8
	12	70	60	0	11
	Ave.	73.3	**46.6**	**0**	8.6
Under mangrove canopy (140m)	13	80	50	0	0
	14	80	55	0	0
	15	80	80	0	0
	Ave.	80	**61.6**	**0**	**0**
Edge of dieback area (145m)	16	0	20	0	0
	17	1	0	0	0
	18	18	0	0	0
	Ave.	6.3	**6.6**	**0**	**0**
Dieback (ponded) area (150m)	19	20	0	0	0
	20	5	0	0	0
	21	19	0	0	0
	Ave.	14.6	**0**	**0**	**0**

The volume discharged has increased significantly in recent years in response to an increasing population in the bayside area.

A preliminary survey of the Whyte Island mangal was undertaken during a 0.52 m tide on the 24th February 2005 to assess both algal/cyanobacterial populations and mangrove dieback. A more detailed survey was undertaken during a 0.31 m tide on the 19th July 2005 when algal/cyanobacterial populations are more abundant and floating algal drifts are known to occur (R. Morton, pers. com).

RECORDING VEGETATION

Vegetation was recorded along a transect through the mangal extending from the seaward edge, approximately 10 m south of the

Table 4. Macroalgal species recorded from the Whyte Island mangal.

Cyanobacteria

Lyngbya majuscula (Dillwyn) Harvey

Microcoleus chthonoplastes (Mertens) Zanardini

Chlorophyta (green algae)

Cladophora socialis Kützing

Rhizoclonium riparum (Roth) Harvey

Ulva compressa L.

   (= *Enteromorpha compressa* (L.) Nees)[1]

Ulva flexuosa Wulfen

   (= *Enteromorpha flexuosa* (Wulfen) J.Ag.)[1]

Ulva lactuca Linnaeus

Ulva ralfsii LeJolis

   (= *Enteromorpha ralfsii* Harvey)[1]

Rhodophyta (red algae)

Bostrychia moritiziana (Sonder ex Kützing) J. Agardh[2]

Bostrychia radicans (Montagne) Montagne[2]

Bostrychia simpliciuscula Harvey ex J. Agardh

   (=*B. tenuissima* R.J. King & Puttock)[3]

Bostrychia tenella (Lamouroux) J. Agardh

Caloglossa adhaerens King and Puttock

Caloglossa ogasawaraensis Okamura

Caloglossa viellardii (Kützing) Setchell[4]

Catenella nipae Zanardini

Gracilaria sp.

Murrayella periclados (C. Agardh) Schmitz

Polysiphonia infestans Harvey

Polysiphonia sp.

Sarcomena filiforme (Sonder) Kylin (drift)

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[1]Based on DNA sequencing, the genus *Enteromorpha*, often a signature genus in disturbed areas, has been reduced to a synonym of the genus *Ulva* (Hayden *et al.* 2003).

[2]Zuccarello & West (2003) treated *Bostrychia radicans/B. moritiziana* as a species complex.

[3]Zuccarello & West (2006) treated *Bostrychia tenuissima* as a synonym of *Bostrychia simpliciuscula*

[4]Kamiya *et al.* (2003) treated most Eastern Australian *Caloglossa leprieurii* as *Caloglossa viellardii*.

mouth of Crab Creek, to an area of mangrove dieback at the landward edge (Fig. 3). The algal/cyanobacterial vegetation was recorded from 0.25 m² replicate quadrats systematically placed on the transect, and at a 5 m interval to each side. Each recording station was selected when changes in the algal vegetation were detected. For each quadrat, quantitative estimates of individual algal/cyanobacterial species abundance were made using the 5 point ordinal scale of Hult-Serander-Du Rietz based on percentage vegetation cover (1: <6.25%; 2: 6.25–12.5%; 3: 12.5–25%; 4: 25–50 %; 5: 50–100%; Du Rietz 1921). For the purposes of species identification, samples of the algal/cyanobacterial vegetation were collected for light microscopy examination ranging in magnification from X10 to X400. Pneumatophore number, water depth, overhead mangrove canopy cover, mangrove seedling number and any drift algal/cyanobacterial material were also recorded for each quadrat. Three replicate quadrats were surveyed at 4 stations/vegetation types on the 24th Feb 2005 and at 8 stations/vegetation types on 19th July 2005 (Table 1).

RESULTS

Loss of mangal was apparent in two large areas flanking the east side of Port Drive at the landward side of the mangal. Even under the mangal canopy adjacent to the dieback areas, there were many dead mangrove trunks and branches scattered over the mangal floor. Pneumatophore numbers were greater under the mangrove canopy than in the dieback area (Tables 2, 3) and, in February, under the canopy peripheral to the dieback area (Table 2). The seaward fringe (to 15 m) had greater canopy cover (70–80%) than other areas of the mangal. Ponding of water in the dieback area contrasted with only a slight covering of water (generally up to 1 cm depth) under the mangrove canopy during the higher low tide of the February survey. Recruitment of mangrove seedlings was only recorded under the mangrove canopy 40–80 m away from the seaward edge (Tables 2, 3). No seedling recruitment was recorded in the dieback areas. There was very little algal/seagrass drift observed during the surveys. Some detached thalli of the red alga *Sarcomena filiforme* were

Table 5. Cover of algal species in the Whyte Island mangal, 24th Feb 2005. (1 = <6.25%; 2 = 6.25–12.5%; 3 = 12.5–25%; 4 = 25–50 %; 5 = 50–100% cover). (shaded quadrats not sampled). Canopy cover at 'Edge of Dieback' varied from 0–60% (see Tables 2 and 3).

Canopy present (C)	Yes			Yes		Yes				Yes			Yes			Yes			Edge of dieback			No		
Distance from Sea (m)	0			15		40				80			140			145			150			150		
Species/Quadrat No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Bostrychia tenella				1	1	1	1		1															
Bostrychia moritziana					1																			
Caloglossa adhaerens				1																				
Caloglossa ogasawaraensis				1			1	1	1				1	1	1									
Catenella nipae				2	2										1									
Gracilaria sp.				1		1																		
Microcoleus chthonoplastes																			5	5	5			
Murrayella periclados				1		2	2																	
Ulva lactuca				2	2				2															

trapped among pneumatophores on the seaward side of the mangal and small amounts of dead seagrass leaves were caught on some mangrove branches.

A total of 19 algal (6 species of Chlorophyta and 13 species of Rhodophyta) and 2 cyanobacterial species were recorded from the Whyte Island mangal over the 2 surveys (Table 4). Many species grew on the Avicennia marina pneumatophores although some (e.g. Gracilaria) were found growing on the mud. Lower species richness and abundance were recorded during the February survey compared with the July survey (Tables 5, 6). Caloglossa adhaerens, recorded in the February survey, is rare in mangals of Moreton Bay.

Two vegetation types were identified along the transects: a benthic microbial mat (and in July unattached Ulva compressa) in, and near, the dieback area and an assemblage of red and green algal species under the mangal canopy (Tables 5, 6). The microbial mats were dominated by the filamentous cyanobacterium Microcoleus chthonoplastes which, although restricted in distribution to the ponded area, was the most abundant of all the species recorded along the transects in both February and July. Large free-floating thalli of the green alga Ulva compressa were often tangled around pneumatophores on the edges of the ponded area in July. In February, the macroalgal community under the mangal canopy was characterised by widespread low cover of Caloglossa ogasawaraensis and to a slightly lesser extent Bostrychia tenella, and a more restricted distribution but greater cover of Catenella nipae and Ulva lactuca (Table 5). More species were common under the canopy in July when species of the red algal genera Bostrychia, Caloglossa, Catenella, Gracilaria and Murrayella were well represented while species of the green algal genera Ulva, Rhizoclonium and Cladophora were less abundant (Table 6).

DISCUSSION

The 21 macroalgal/cyanobacterial species recorded from the Whyte Island mangal is less than the 35 marine macroalgal species previously reported for mangals throughout Moreton Bay (Cribb 1979), but is similar to the total

Table 6. Cover of algal species in the Whyte Island mangal, 19th July 2005. (1 = <6.25%; 2 = 6.25–12.5%; 3 = 12.5–25%; 4 = 25–50%; 5 = 50–100% cover). Canopy cover at 'Edge of Dieback' varied from 0–60% (see Tables 2 and 3).

Canopy present (C)	Yes			Yes			Yes			Yes			Yes			Yes			Edge of dieback			No		
Distance from Sea (m)	0			15			40			80			140			145			150			150		
Species/Quadrat No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Bostrychia tenella							1	1		1	1	1	1	1	1									
Bostrychia moritziana			1	1			1	1		1	1	1	1	1										
Bostrychia radicans				1				1																
Bostrychia simpliciuscula	1		1	1	1	1	1	1		1	1	1	1											
Caloglossa ogasawaraensis	1			1	1	1	1	1		2	1	1	1	1	2									
Caloglossa vieillardii						1					1		1											
Catenella nipae					1		2	2	2															
Cladophora socialis			1	1	1																			
Gracilaria sp.							3	2	3	1	1	1												
Lyngbya majuscula					1																			
Microcoleus chthonoplastes																5	5	5	5	5	5			
Murrayella periclados			1	1	1		1	1		1	1	1												
Polysiphonia sp.						1				1		1												
Polysiphonia infestans			1																					
Rhizoclonium riparium				1	1							1	1	1										
Sarcomena filiforme	5		1			5																		
Ulva compressa		3																	2	2	1	4	3	5
Ulva flexuosa										1														
Ulva lactuca	1				1		1	1						1										
Ulva ralfsii					1			1			1													

number of macroalgal/cyanobacterial species recorded for the mangals of nearby Serpentine Creek (Atherton & Dyne 1977). However, each of the four seasonally sampled Serpentine Creek transects recorded between 9 to 13 species, a species richness consistent with the February survey for Whyte Island but considerably lower than that reported for the July survey. The reason for the lower species richness at the Serpentine Creek sites is not known, although mangals lining creeks may support fewer macroalgal/cyanobacterial species than mangals directly under a fully marine influence, as has been reported previously for southern Australian mangals (Davey & Woerlkerling 1980). Sewage from the Luggage Point outfall may also have had an impact on macroalgal species diversity at Serpentine Creek. Cribb (1979) also reported 13 cyanobacterial species from saltmarshes and mangals of Moreton Bay, but gave no ecological distribution data except to report that *Lyngbya majuscula* (as *Microcoleus lyngbyaceus*) and *Schizothrix* spp. were common on mud substrata between salt marshes and mangals, an area of the shore only wetted by spring tides. Like other mangals in Australia and around the world, species of the red algal genera *Bostrychia*, *Caloglossa*, *Catenella*, *Gracilaria* and *Murrayella* were present under the canopy at Whyte Island (King & Puttock 1994; Phillips *et al.* 1994; Laursen & King 2000). The presence of *Caloglossa adhaerens*, a rare species in Moreton Bay, together with differing distribution patterns of the mangal macroalgae at various sites in Moreton Bay highlights the pressing need to collect quantitative data on these species for the purposes of documenting biodiversity and for developing strategies for macroalgal conservation. Further, it is imperative that the data collected incorporates recent taxonomic revisions of mangrove species (see footnotes in Table 4).

Shifts in macroalgal species composition and abundance are considered invaluable tools for assessing the responses of marine communities to natural and anthropogenic-mediated disturbances (Middelboe *et al.* 1997, 1998; Middelboe & Sand-Jensen 2000; Pedersen & Snoeijs 2001; Eriksson *et al.* 2002). Lower abundances of red algal species, the presence of green algal species under the mangal canopy and of the benthic *Microcoleus chthonoplastes* mat in the ponded area

are features which separate the macroalgal/cyanobacterial vegetation of Whyte Island from other mangals in the Moreton Bay region (J. Phillips, pers. observ.). Large ponded areas are usually not found in the mangals of Moreton Bay, the landward edge of which usually grades either into salt marsh, also previously reported by Cribb (1979), or grassland in residential areas or directly into industrial sites (J. Phillips, pers. observ.).

Species of the red algal genera *Bostrychia*, *Caloglossa*, *Catenella*, *Gracilaria* and *Murrayella* generally account for < 10% cover in most quadrats in the Whyte Island mangal, contrasting markedly to healthy mangals in Moreton Bay where red algal cover frequently exceeds 20% (J. Phillips, pers. observ.). *Catenella nipae* and *Bostrychia tenella* are often dominant species which are conspicuous, identifiable in the field, and festoon pneumatophores on the seaward edge and from the middle to the landward edge of the mangals respectively (J. Phillips, pers. observ.). The lower abundances of red algal species at Whyte Island are probably related to the altered environmental conditions of the incomplete canopy. These red algal species are well adapted to the tidally-driven immersion-emersion cycles of the mid to upper intertidal zone, but they are still dependent on the shading effects of the canopy to ameliorate the higher light intensities, temperature, desiccation and osmotic stress associated with long periods of emersion (Davison & Pearson 1996). These environmental stressors are considerably less under intact canopies than for areas outside or under breaks in the canopy (Clarke & Hamon 1969; Hutchings & Saenger 1987; Pena *et al.* 1999). Mangal red algal species are typical 'shade plants' with low light adaptations for the saturation of photosynthesis and low light compensation points (below 17 μmol photons m^{-2} s^{-1}) (Karsten & Kirst 1989; Karsten *et al.* 1993; Pena *et al.* 1999). Consequently mangrove red algae are prone to photoinhibition and photodamage at ambient irradiances as low as 200 μmol photons m^{-2} s^{-1} (~ 10% sunlight) (Pena *et al.* 1999). Consistent with this are the lower species richness and abundance of mangal red algae recorded in February at Whyte Island which in part would be due to the higher light intensities of summer.

Species of the green algal genera *Ulva*, *Cladophora* and *Rhizoclonium*, found under the canopy within the Whyte Island mangal, have not been observed under the canopy inside other mangals in the Moreton Bay region (J. Phillips, pers. observ.). Green algal species are usually common on the outside edges of mangals (Atherton & Dyne 1977; Cribb 1979; Hutchings & Saenger 1987), but are rare within mangals, presumably limited by the low light intensities under an intact canopy. The higher light intensities under the breaks in the canopy and in the ponded area as well as the elevated nutrient levels from the sewage discharge would favour rapid-recruiting, opportunistic, stress-tolerant species of *Ulva*, *Cladophora* and *Rhizoclonium* (Brown *et al.* 1990; Duarte 1995; Morand & Briand 1996; Hernandez *et al.* 1997; Raffaelli *et al.* 1998; Taylor *et al.* 2001) over less tolerant species, and may explain the higher abundance of stress tolerant species inside the Whyte Island mangal. Elevated nutrient levels from effluent discharge have undoubtedly contributed to the shift in macroalgal species composition at the disturbed sites within the Whyte Island mangal.

The presence of the benthic microbial mat dominated by the cyanobacterium *Microcoleus chthonoplastes* is indicative of the harsh environmental conditions prevailing in the ponded area. Loss of the mangrove canopy, which would have a moderating effect on the physical environment, would result in higher light intensities and temperatures in the ponded area, favouring tolerant cyanobacterial species (Sage & Sullivan 1978; Golubic 1994; Potts 1999; Bhaya *et al.* 2000; Golubic *et al.* 2000; de Lomas *et al.* 2005). *Microcoleus chthonoplastes* often dominates intertidal and lagoonal microbial mats in temperate to tropical marine habitats worldwide (Potts 1980, 1999; Prufert-Bebout & Garcia-Pichel 1994; Stal 2000). This species is desiccation tolerant, surviving prolonged periods of emersion (Hershkovitz *et al.* 1991; Potts 1999), due to the production of a water-retentive mucilaginous sheaths (Stewart 1977; Hussain & Khoja 1993; DeWinder *et al.* 1999; Stolz 2000) and the ability to move to deeper mat layers, where the species is also shaded from the damaging effects of high light intensity and UV radiation (Stewart 1977; Ramsing & Prufert-Bebout 1994; Bebout & Garcia-Pichel 1995; Stal 2000).

McLeod (1969) recorded *Microcoleus chthonoplastes* as a minor component of southern Queensland salt marshes but the species has not previously been recorded from mangals in the Moreton Bay region. This again reflects the paucity of knowledge of the ecology of this region, and in this instance of cyanobacterial diversity. *Microcoleus chthonoplastes* has been recorded from tropical Queensland (Phillips 1997, 2002), from mangals in the Sydney region (Karsten 1996) and in mangals worldwide (Fogg 1973; Tanaka & Chihara 1984; Lambert *et al.* 1989; Hussain & Khoja 1993; Phillips *et al.* 1994), occuring either as an inconspicuous component on aerial roots (Phillips *et al.* 1994) or conspicuously on mud and aerial roots (Fogg 1973; Lambert *et al.* 1989) or in microbial mats (Potts 1980; Stal *et al.* 1985; Hussain & Khoja 1993).

POSSIBLE CAUSES OF MANGROVE DIEBACK

It is apparent from this survey and the WBM (2002) report that the Whyte Island mangal is under threat. While the loss of *Avicennia marina* trees from and the occurrence of large areas of *Microcoleus chthonoplastes* mats in the ponded area are obvious features of the environmental stress, the mangroves and macroalgae at the landward edge of the existing Whyte Island mangal are also showing signs of stress. This is evident from the large gaps in the canopy, restricted recruitment of mangrove seedlings (which never exceeded the 6 leaf stage), epicormic shoots on *Avicennia marina* trunks, the reduced biomass of the Bostrychia/Caloglossa association on pneumatophores and the presence of green algae under the mangrove canopy.

It is probable that interactions of multiple stressors may have contributed to the mangal dieback over the last three decades at Whyte Island. Mangroves live in saline, waterlogged, anaerobic soils and already are hard pressed to cope with salt toxicity, absorption of water against an osmotic gradient (desalination), high light regimes, high temperatures and anaerobiosis (Clough *et al.* 1982; Hutchings & Saenger 1987; Saenger 2002). Any disturbance will interfere with the finely-tuned balance between the mangroves and the environment that supports them, often resulting in a loss of trees and a decline in the mangal. It makes good sense to start by examining some of the more obvious

potential causes of the Whyte Island dieback: 1) the large scale ponding of seawater within the area formerly occupied by the mangal; 2) discharge of sewage into Crab Creek; and 3) the potential for onshore algal blooms or drifts from offshore blooms to smother *Avicennia* pneumatophores and/or contribute to, or cause, seawater ponding.

Ponding of water. Mangroves do not survive in habitats which are flooded for prolonged periods, and for this reason are ecologically restricted to the upper intertidal zone (mid to high tide mark), an area where the substratum should be drained at every low tide. Mangal soils are typically anaerobic, the mangrove roots obtaining oxygen for respiration from the atmosphere via aerial roots. Diffusion of air during low tide through air pores (lenticels and horizontal structures) on *Avicennia marina* pneumatophores is sufficient to aerate the extensive aerenchyma (air filled tissue) throughout the pneumatophore/subterranean cable root system in order to supply oxygen for root respiration during tidal inundation (Curran 1985; Curran *et al.* 1986; Skeleton & Allaway 1996). Root respiration, required for the energetically-expensive uptake of water against the osmotic gradient (desalination), is dependent on oxygen stored in root aerenchyma, as there is little oxygen in the surrounding anaerobic muddy substratum. Oxygen is rapidly consumed by *Avicennia marina* roots, with only c. 0.1 atmospheric oxygen concentration remaining in the root aerenchyma 22 hrs after the onset of the continuous flooding (Skeleton & Allaway 1996). Continuous immersion of aerial roots was considered responsible for the death of mangroves at Wallum Creek, North Stradbroke I., following the construction of a 70 m long bund wall which retained water in the mangal (Quinn & Beumer 1984). Waterlogged mangroves behind bund walls generally die within six weeks of inundation (Hutchings & Saenger 1987; Saenger 2002). Death of mangroves also followed the unintended ponding of seawater from roads constructed through mangals in northern Western Australia (Gordon 1987), New Guinea (Saenger 2002), Puerto Rico (Patterson-Zucca 1982) and Colombia (Elster *et al.* 1999).

Sewage discharge. Several studies have investigated the discharge of secondarily-treated sewage into mangals, reporting that mangroves have the ability to absorb high levels of nutrients found in sewage without any discernible harmful effects (Nedwell 1975; Clough *et al.* 1983; Corredor & Morell 1994; Tam & Wong 1995; Wong *et al.* 1995; Saenger 2002). However, sewage sludges may be contaminated with heavy metals which can be mobilised and released from mangal sediments (Montgomery & Price 1979; Tam & Wong 1997). Heavy metals may be accumulated by mangrove species (Clark *et al.* 1997, Lacerda 1998), although detrimental effects to mangrove species, which are generally considered to have a high tolerance to heavy metal exposure and accumulation, have not been observed even after exposing seedlings to sediment concentrations of Cu, Zn, Pb, Ca and Hg to approximately 500 µg g^{-1} (for discussion see Saenger 2002). The sediments at Whyte Island have heavy metal concentrations well below 100 µg g^{-1} (WBM 2002).

While nutrients and heavy metals appear not to have any discernible effect on mangroves, sewage effluent may also be the source of anionic surfactants (found in detergents), plasticizers and other toxicants such as phenol, toluene and chlorine. These components may be delivered in pulses of high, potentially-damaging concentrations, may act synergistically with other components to either enhance\reduce toxicity (Kevekordes 2001) or may interact with the physical environment, such as the sediments, resulting in the development of adverse environmental conditions (e.g. the production of acid sulphate soils due to the oxidation of sulphides bound to heavy metals (Clark *et al.* 1997)).

Algal blooms and drifts. Marine macroalgal blooms and drifts are often a consequence of environmental disturbance caused by elevated nutrient levels delivered, in the case of Whyte Island, from sewage effluent. Effluent from the Wynnum North Sewage Treatment Plant is discharged directly into Crab Creek and under favourable environmental conditions could potentially result in on-site blooms. Effluent is also discharged from Luggage Point and from rivers feeding into Moreton Bay. These more distant sources may result in offshore blooms drifting into the Whyte Island mangal. However, these were not observed during the present study. The small amount of macroalgal biomass recorded under the canopy at Whyte Island would not be sufficient to form floating blooms. Nor are there any reports in the scientific literature of the very

common *Microcoleus chthonoplastes* forming floating mats, although the benthic mat formed by this species in the ponded area could prevent or further exacerbate poor seawater drainage at low tide, due to the ensheathing mucilage around the cyanobacterial filaments (Golubic 1973).

Algal/cyanobacterial blooms and drifts were not observed during the current study at Whyte Island, but monitoring would be required to detect these episodic events. Large drifts of *Ulva* are known to occur at Whyte Island during the winter (R. Morton, pers. com.) and drifting algal mats have been reported to block drainage channels and cause the ponding of water at Luggage Point (WBM 2002). Atherton & Dyne (1977) reported extensive floating algal masses at low tide, dominated by *Gracilaria sp.* and *Ulva clathrata* and to a lesser extent *Caulerpa fastigiata* during summer near thin stands of stunted mangroves at Serpentine Creek. They also reported vast tracts of floating cyanobacterial mats comprising *Lyngbya majuscula*, *Scytonema* and *Chroococcus* caught on pneumatophores further landward of the floating macroalgal masses. Any impact the drift may have had on the mangroves was not described, and the authors found it difficult to assess whether algal mat growth had been stimulated by mangrove thinning, also reported in their study.

There is little evidence on the effects that algal/cyanobacterial/seagrass drifts may have on mangrove survival. Bird & Barson (1982) reported that accumulations of dead *Zostera* were thought to contribute to mangrove dieback in Westernport Bay, Victoria. Loss of mangroves in the St Kilda-Port Gawler area of South Australia was attributed to large drifts of *Ulva* and dead seagrass retarding recruitment of *Avicennia marina* seedlings and smothering pneumatophores (Edyvane 1995).

RECOMMENDATIONS FOR FURTHER STUDY

While a number of factors may potentially interact to cause mangrove dieback, the long periods of seawater inundation (several days to weeks) of the Whyte Island mangroves would itself be sufficient to cause mangrove death. Thus investigations should initially focus on the ponding of water. Gaining an understanding of the environment in the ponded area is neces-

sary for devising a rehabilitation plan. Restoring vegetation on the tidal landward fringe is challenging because of natural environmental stresses and anthropogenic disturbances. The impact of strandings of large masses of algae or cyanobacteria, that may contribute both to water ponding and to pneumatophore smothering, also needs investigation.

The following research is suggested:

1. The ponded area should be studied in regard to physico-chemical parameters, the periodicity of inundation from the sea, freshwater inputs, water depth, the biology of the *Microcoleus chthonoplastes*, and mangrove recruitment (if any). The study should be undertaken throughout the year to detect seasonal effects and tidal variation (both lunar and solar cycles).

2. Possible impacts of algal/cyanobacterial blooms/drift on mangrove survival at Whyte Island need to be investigated and monitored (in particular the occurrence, periodicity, origin (inside versus outside mangal), species composition, and possible causes). Identifying the species composition of any blooms/drifts is crucial for identifying the possible origin of the bloom species. This in turn will determine appropriate management strategies. In our opinion, blooms that may impact on the Whyte Island mangal will be unlikely to originate from within this mangal. Similarly a variety of species also form 'algal/cyanobacterial mats', and the likelihood that *Microcoleus chthonoplastes* mats may become pelagic also needs to be investigated.

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The seagrass *Halophila minor* newly recorded from Moreton Bay

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ABSTRACT

The seagrass *Halophila minor* (Zoll.) Hartog is recorded for the first time from Moreton Bay on the subtropical east Australian coast. *H. minor* (under the name *Halophila ovata* Gaud.) has previously been widely reported from tropical Australia, but this record marks a significant southward range extension. The establishment of *H. minor* in southern Moreton Bay may be a recent event, with its southerly dispersal mediated by the effects of climate change, and a more strongly flowing East Australian Current. However it is also probable that *H. minor* had simply been overlooked or misidentified in the past because of its superficial resemblance to a small morph of the morphologically-variable and very common *Halophila ovalis* (R. Br.) Hook f. ❏ *biogeography, first record, Halophila minor, Halophila ovalis, Halophila ovata, southern Moreton Bay. seagrass, Southport Broadwater.*

As with many semi-enclosed coastal marine environments on the Australian east coast, the Southport Broadwater supports extensive seagrass communities on predominantly sandy substrata. As part of a survey in this area conducted from May to July 2006 by the environmental consultant company GHD Pty Ltd for the Queensland Department of Natural Resources, collections were made of a small seagrass species that we later identified as *Halophila minor* (Zoll.) Hartog. Three *Halophila* species have been previously recorded from Moreton Bay: *Halophila ovalis* (R. Br.) Hook f. and *Halophila spinulosa* (R. Br.) Asch. are widely distributed throughout the Bay, while *Halophila decipiens* Ostenf. inhabits turbid southern Bay waters, and mainland coastal localities such as Raby Bay, Waterloo Bay, Deception Bay and Pumicestone Passage (Young & Kirkman 1975;

Hyland *et al.* 1989). The present note serves as the first formal record of the occurrence of *H. minor* on the subtropical east Australian coast.

Voucher specimens of Southport *H. minor* have been lodged in the Queensland Herbarium. First collections of *H. minor* were made from the Labrador foreshore between Loders and Biggera Creeks (27°56′34.3″ S 153°24′57.7″ E) where it grew in a 9.4 ha upper-subtidal seagrass community dominated by *Z. capricorni*, with *H. ovalis* and *Halohide uninervis* subdominant (Fig. 1).

A second upper-subtidal seagrass community dominated by *H. minor* and *Z. capricorni* grew on the northwestern shoreline of a large sandbank south of Wavebreak Island. Together with a *Z. capricorni/H. ovalis* community on the southwestern part of this sandbank, the seagrasses covered an area of 27 ha. This sandbank is

FIG. 1. Habitat map of seagrass communities in the Southport Broadwater. (Image courtesy of GHD Pty Ltd and the Queensland Department of Natural Resources).

relatively close to the Gold Coast Seaway, a coastal engineering modification to the Southport Bar, and would be flushed with relatively clean oceanic seawater. Considerable sand movement has occurred over the last two decades with the sandbank attaining its greatest areal extent in 2006 (this study), although also being greater in extent in 1987 (Hyland *et al.* 1989) than in 1997 (McLennan & Sumpton 2005). In addition to natural disturbance (tidal movements, storms), sand movements would also be increased in the shallow waters by recreational boat traffic and jet skis. Abundance of *H. minor* in Broadwater localities with mobile sands is consistent with the observation (as *H. ovata*) that it occurred as the dominant pioneer species following destruction of seagrass communities on Magnetic Island by Cyclone Althea in 1971 (Birch & Birch 1984). *H. ovata* is a high stress/high disturbance species, tolerant of variations in sediment depth and degree of emersion, but intolerant of competition from other seagrass species (Birch & Birch 1984).

TAXONOMIC HISTORY

The genus *Halophila* comprises 5 sections and 15 species, with 10 species assigned to the section *Halophila* (den Hartog & Kuo 2006). Species in the section *Halophila* have short erect shoots bearing a pair of leaves, and are taxonomically separated from each other by differences in leaf size, shape, and pattern of venation. These characters may be variable and consequently species delimitation, particularly for *Halophila ovalis* (R. Br.) Hook. f., remains problematical. Den Hartog (1970) considered *H. ovalis* to be a species complex, but recognised *Halophila ovata* Gaudichaud (1826) as a separate entity, and reduced *Halophila minor* (Zoll.) Hartog, described in 1854, to a synonym of *H. ovata*. The name '*H. minor*' was later resurrected by Sachet & Fosberg (1973) who reported that Gaudichaud (1826) considered *H. ovata* to be the same species as *H. ovalis*, described in 1810. Sachet & Fosberg (1973) pointed out that under the rules of the International Code of Botanical Nomenclature (Article, 63), *H. ovata* is a superfluous name, therefore illegitimate, and a synonym of *H. ovalis*. Most seagrass ecologists have been unaware of this nomenclatural clarification, and have continued to use the name, *H. ovata* (Birch & Birch 1984; Lanyon 1986; Walker & Prince 1987; Coles *et al.* 1987, 1989; Poiner *et al.* 1987, 1989; Lee Long *et al.* 1993), although some authors have referred to it correctly as *H. minor* (McMillan 1986; Kuo & McComb 1989).

In a more recent study of herbarium specimens, including type material and new collections, Kuo (2000) concluded that *H. minor* and *H. ovata* are separate species, distinguished by differences in the number of lateral veins and in the distances between adjacent veins and between the intra-marginal vein and the leaf margin. *Halophila ovata* has been renamed *Halophila gaudichaudii* J. Kuo (Kuo *et al.* 2006) and has a known geographical distribution restricted to the north western Pacific Ocean localities of Saipan, Guam, Yap (Micronesia), Manila Bay (Philippines) (Kuo 2000; den Hartog & Kuo 2006) and Okinawa (Kuo *et al.* 2006).

DISTRIBUTION OF *HALOPHILA MINOR*

Halophila minor is widely distributed in the tropical Indian (Kenya, India, Malaysia, Western Australia) and the western Pacific Oceans (den Hartog & Kuo 2006: 13). As *H. ovata* it has been previously recorded in tropical northeastern Australia (den Hartog 1970; Birch & Birch 1984; Lanyon 1986; Coles *et al.* 1987, 1989; Poiner *et al.* 1987, 1989), as far south as Townsville (den Hartog 1970). The present new record extends the geographical range about 1000 km south to the Southport Broadwater.

Previous records of *H. minor* at several localities from Townsville south to Hervey Bay (Lee Long *et al.* 1993) require confirmation, particularly as the species (as *H. ovata*) received little attention in that publication (listed in Table 2), and the significant putative range extension was not discussed with the geographical distribution of other seagrass species. Furthermore, other studies in Hervey Bay (Preen *et al.* 1995) or in nearby waters (Dredge *et al.* 1977), have not reported *H. minor*. If *Halophila minor* occurred in Hervey Bay, it should have flourished, colonising as the pioneer species to form monospecific communities in denuded areas (Birch & Birch 1984), following the bay-wide destruction of seagrass communities after the floods and cyclone of 1992 (Preen *et al.* 1995). It is also
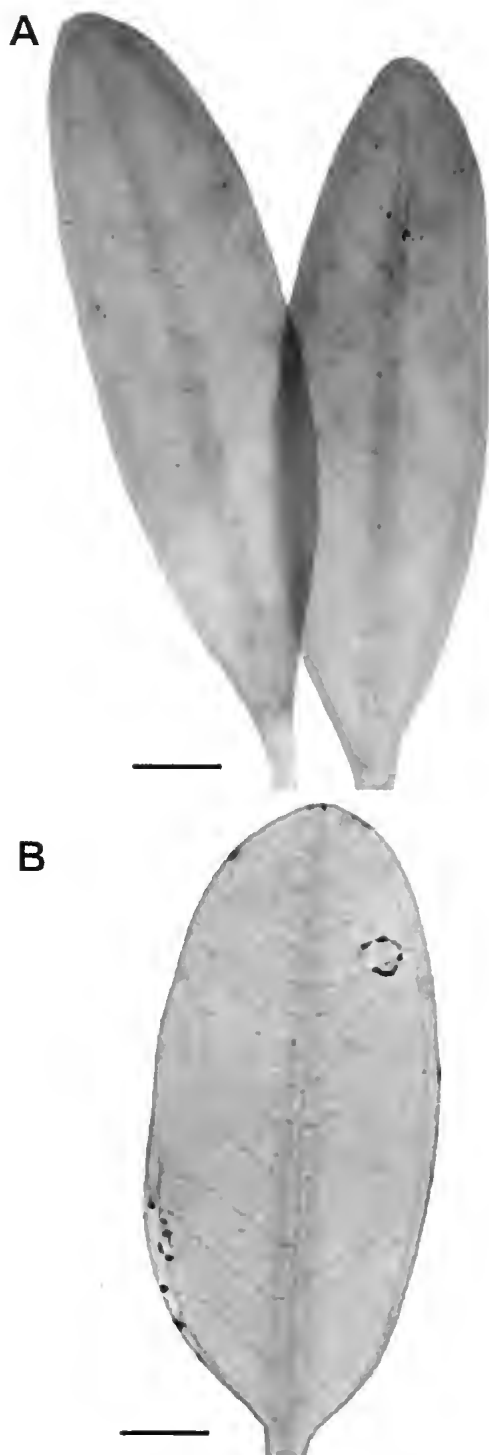
possible that *H. minor* has a similar disjunct geographical distribution to the tropical sea-grasses *Syringodium isoetifolium* (Asch.) Dandy and *Cymodocea serrulata* (R.Br.) Asch. & Magnus which have southern outlier populations in Moreton Bay, approximately 500 km from the nearest populations of these species in Shoal-water Bay (Lee Long *et al.* 1993).

IDENTIFICATION

Southern Moreton Bay specimens agree with the recent revision of the species concept of *H. minor*, with the exception of the linear to oblanceolate leaf blades for the local material compared to the ovate blades of other popula-tions of *H. minor* (Kuo, 2000; Kuo & den Hartog, 2001) (Table 1). The Broadwater plants were mature, evident from the long petioles (1–1.5 cm in length). Macroscopically, the narrow leaf blades of *H. minor* superficially resemble those of the small morph of *H. ovalis* but are easily differentiated from the broader (> 5mm broad) elliptic to obovate to ovate blades of the large morph of *H. ovalis* (den Hartog 1970; Kuo & McComb 1989). However, 10 to 25 pairs of lateral veins typically arising from the mid rib at more or less regular intervals in *H. ovalis* clearly distinguishes Broadwater *H. minor* in which 4 to 9 often unpaired lateral veins arise at irregular intervals from the midrib (Fig. 2A,B). The smaller number and lack of pairing of veins are clearly illustrated for tropical Queensland specimens of *H. minor* (Fig. 9, Lanyon 1986) but the presence of unpaired veins arising at irregular intervals from the midrib appears not to have been previously used as a taxonomic character to distinguish *H. minor*.

DISCUSSION

The occurrence of *H. minor* in the Southport Broadwater may represent a recent range expan-sion, with dispersal further south mediated by the effects of climate change and a more strongly flowing East Australian Current (Cai *et al.* 2005). This contention is consistent with the observations that previous surveys of the Southport Broadwater (Kirkman 1975; Hyland *et al.* 1989; McLennan & Sumpton 2005) did not record *H. minor* and that the species is considered to be tropical (den Hartog 1970; den Hartog & Kuo 2006: 13), also supported by the

FIG. 2. **A**, leaf of *Halophila minor* showing 8–9 largely unpaired veins arising from the mid vein. Scale = 0.8 mm. **B**, Leaf of *Halophila ovalis* with 13 pairs of lateral veins. Scale = 2 mm.

Table 1. Diagnostic characters for *Halophila minor*. Data in first column is based on a sample of 10 leaves from Moreton Bay samples (this study); data in second is taken from Kuo (2000).

Characters	Moreton Bay *Halophila minor*	*Halophila minor* (Kuo 2000)
Lamina length (mm)	6–8	6–12
Lamina breadth (mm)	1.7–2.8	3.5–6.0
Number of lateral veins	4–9	(4) 7–12 (13)
Distance between lateral veins (mm)	0.42–0.75	0.65–0.85
Distance between intramarginal vein and lamina margin (mm)	0.15–0.19	0.15–0.19

fact that all Queensland specimens of *H. minor* in the Queensland Herbarium have been collected in the tropics (Henderson 2002). However, it is equally plausible that *H. minor* has always been present in Moreton Bay but has been overlooked or included in *H. ovalis*, an ecologically common and geographically widespread species which ranges in Australia from the tropics to temperate Cowaramup Bay in Western Australia (Robertson 1984; Hillman *et al.* 1995) and to Mallacoota on the eastern Australian coast (West *et al.* 1989; Harden 1990). *Halophila ovalis* exhibits considerable morphological plasticity with respect to leaf shape and size (den Hartog 1970; Young & Kirkman 1975; Robertson 1984; Poiner 1984; Poiner *et al.* 1987), occurring in Moreton Bay as two statistically significant size morphs differentiated by leaf breadth: the small morph of the intertidal zone with a blade breadth < 5mm and the large subtidal morph with a blade breadth > 5mm (Poiner 1984). As leaf breadth is one of the characters used to separate *H. minor* from *H. ovalis* (Lanyon 1986; Poiner *et al.* 1987; Kuo & McComb 1989), and the only visible character for field identifications, it is reasonable to suggest that Moreton Bay *H. minor* may have been misidentified as the narrow morph of *H. ovalis*. Some ecological surveys (Birch & Birch 1984; Poiner *et al.* 1987) have avoided the problem of distinguishing co-occurring *H. minor* from narrow *H. ovalis* in the field by presenting combined data for the two species.

Future seagrass surveys of the Australian east coast should endeavour to examine narrow-leaved *Halophila* plants microscopically to distinguish narrow *H. ovalis* from *H. minor*. Further taxonomic studies are required to clearly define species boundaries for *H. ovalis* and *H. minor* for the purposes of accurate species identification. This study clearly demonstrates the importance of lodging voucher specimens in herbaria in order to verify the identity of species reported by ecological surveys.

ACKNOWLEDGEMENTS

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Marine cyanobacterial, algal and plant biodiversity in southeast Queensland: knowledge base, issues and future research directions

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ABSTRACT

Cyanobacteria, algae, seagrasses and mangroves contribute significantly to marine ecosystem function in their roles as primary producers underpinning marine food webs, as 'ecosystem engineers' providing habitat, and in modulating global biogeochemical cycles and stabilising shorelines. Species-level knowledge for these organisms in southeast Queensland varies greatly, with the relatively few seagrass and mangrove species well studied compared to the underdescribed and undersampled algae and cyanobacteria. Algal/cyanobacterial species richness for the region is high but data on biodiversity patterns of these organisms and the ecological processes that cause, maintain and regulate these patterns are dismally incomplete. There are no comprehensive algal/cyanobacterial floras for eastern Australia, ensuring that numerous species are difficult to identify with certainty and thus can not be effectively treated in scientific studies. Accurate identification and knowledge of algal/cyanobacterial biology and ecology at the species level are essential prerequisites underpinning biotic surveys, biomonitoring programs and management strategies for algal/cyanobacterial blooms, exotic species, climate change, rare and threatened species and marine protected areas. Research programs documenting species composition and abundance in marine communities and the ecological and geographical distribution of species are urgently required to provide rigorously-collected data on the ecologically-important cyanobacteria and algae in southeast Qld in order to provide the scientific basis underpinning marine environmental management and marine conservation initiatives, particularly biodiversity conservation. The inability to identify species seriously imperils efforts directed towards arresting the irreversible loss of biodiversity. ❏ *cyanobacteria, algae, seagrasses, mangroves, biodiversity, conservation, Australia.*

Although widely acknowledged to exist at multiple levels of biological organisation ranging from genes to ecosystems, it is understanding biodiversity at the species level that plays a central role in our efforts to conserve species and the habitats, ecosystems and biomes in which species live (May 1995; National Research Council 1995; Bianchi & Morri 2000; Mikkelsen & Cracraft 2001; Mace 2004). Biodiversity results from the diversification of species. Species composition generally plays a crucial role in ecosystem dynamics and function (Dayton 1972; Knowlton & Jackson 1994; Jones *et al.* 1997; Tilman 1999; Loreau *et al.* 2001; Altieri *et al.* 2007). Species drive ecological processes which will undergo functional shifts when sets of species are lost or replaced by other species with differing traits and interactions. Biological impoverishment through species loss reduces the resilience of ecosystems to environmental

change, an important concept underpinning the endeavours of conservation biology which aims to protect not only 'iconic species' but also a wide range of species, including many poorly known and often overlooked species (Murphy & Duffus 1996; Mikkelsen & Cracraft 2001; Clarke & May 2002, Roberts *et al.* 2003; Kenworthy *et al.* 2006), many of which contribute greatly to the sustainability of life on Earth (Corliss 2002).

Surprisingly, the great majority of species on Earth are unknown to science (Raven & Wilson 1992; May 1995; Wilson 2000, 2002; Mace 2004; Crisci 2006; Hodkinson & Parnell 2006). Between 1.5 and 1.8 million species have been described, with conservative estimates of 7 to 15 million species yet to be discovered. Thousands of species, both known and unknown, are threatened by an accelerating rate of extinction, correlated to an increasing human population. Loss of two-thirds of all species on Earth is predicted by the end of this century (Raven 2002 and references therein). Unfortunately, our ability to devise science-based action plans to save species from extinction is severely limited by the fragmented knowledge base in which < 1% of described species are estimated to have been studied beyond the meagre essentials of morphology, habitat preference and geographical location (Wilson 2000; Crisci 2006). Biodiversity loss is irreversible, and unfortunately our ignorance of the biota ensures that we are ill-equipped to both understand the significance of its loss, and protect against it (Clarke & May 2002; Dayton 2003).

The pressing need for marine conservation was first recognised by Kaufman (1988) who challenged the then widely accepted scientific and popular belief that marine ecosystems were beyond the deleterious impacts of the human race. We now know that marine ecosystems have been have been dramatically degraded (Ray & Grassle 1991; Norse 1995; Dayton 2003) and continue to be threatened by the over-exploitation of natural resources, increasing habitat alteration and degradation, worsening eutrophication, introduction of alien species and the impacts of global climate change (Norse 1993; National Research Council 1995). Unfortunately, marine ecosystems and marine bio-diversity have been far less studied than their terrestrial equivalents (Kaufman 1988; Murphy & Duffus 1996; Bianchi & Morri 2000; Kochin & Levin 2003; Boudouresque *et al.* 2005), resulting in fragmentary historical data sets on species composition and abundances in marine communities. Also of great concern is the marked lack of recent reliable data on changes in species composition and abundances in many marine systems (Boudouresque *et al.* 1995; Bianchi & Morri 2000; Hiscock *et al.* 2003).

Little is known of the scale and rate of species loss resulting from anthropogenic impacts on marine ecosystems (Kaufman 1988; Carlton *et al.* 1991, Carlton 1993; Norse 1993, 1995; Roberts & Hawkins 1999). Known marine extinctions were limited to relatively few megavertebrate species (Norse 1993; Vermeij 1993), reflecting the difficulty in detecting extinctions of inconspicuous marine species. Furthermore, the full extent of this irreversible biodiversity loss may never be realised because many marine species may have been exterminated before discovery (Roberts & Hawkins 1999; Dayton 2003). The first documented marine invertebrate neoextinction (the eelgrass limpet) was reported 50 years after the event (Carlton *et al.* 1991). Subsequently, several more marine invertebrate neoextinctions have been reported (Carlton 1993; Roberts & Hawkins 1999). Similarly, data on algal extinctions is also sparse, with *Vanvoorstia bennettiana* Harvey last recorded for Port Jackson nearly 150 years ago the only alga regarded as extinct (Millar 2003).

The extent of biodiversity encompassed by cyanobacteria, algae, mangroves and seagrasses is enormous, representing five of the six Kingdoms of Life (Keeling 2004; Palmer *et al.* 2004) (Table 1). Although these phototrophic organisms are commonly referred to as 'marine plants', only the Chlorophyta (green algae) which are the ancestors of the land plants, Rhodophyta (red algae), mangroves and seagrasses belong to the Plant Kingdom. Other algal phyla are assigned to three other Kingdoms with the pro-karyotic Cyanobacteria in the fifth Kingdom. These differing evolutionary histories have profound effects on the biology, physiology and ecology of organisms which must be understood before effective management and conservation initiatives can be devised. Cyanobacteria and algae evolved in and developed

Table 1. Species richness of marine phototrophs. Based on Brodie & Zuccarello 2006 [1]; Williams & Reid 2006 [2]; Saenger 2002 [3]; Den Hartog & Kuo 2006 [4]; Phillips 1998a [5].

Kingdom	Taxa	Estimated described (total species) worldwide	Known species richness in SE Qld
Bacteria	Cyanobacteria	2 000 (?) [1,2]	?
Excavates	Euglenophyta	959 [1,2]	?
Alveolates	Dinophyta (dinoflagellates)	1240 (11 000) [1,2]	?
Chromista	Phaeophyta (brown algae)	1718 (2000) [1,2]	51 [5]
	Chrysophyta (golden algae)	2 400 (5 000) [1,2]	?
	Bacillariophyta (diatoms)	6423 (200 000) [1,2]	?
	Haptophyta (coccolithophorids)	510 (2000) [1,2]	?
	Cryptophyta (cryptomonads)	85 (1200) [1,2]	?
Primoplantae	Chlorophyta (green algae)	3215 (20 000) [1,2]	65 [5]
	Rhodophyta (red algae)	5781 (20 000) [1,2]	161 [5]
	Mangroves	84 [3]	8
	Seagrasses	64 [4]	8

the adaptations necessary for life in aquatic environments. By contrast, mangroves and sea-grasses which colonised the marine environment during the late Cretaceous/ early Tertiary have retained most features characteristic of their land plant ancestors (Saenger 2002; Kuo & Den Hartog 2006). Seagrasses are unique, being the only submarine flowering plants on Earth. Relatively few species of flowering plants (only seagrasses and mangroves) have adapted to life in the harsh environment of the land/sea interface (Table 1).

Approximately 350,000 algal species are estimated to occur on Earth, similar to the species richness for higher plants (World Conservation Monitoring Centre 1992; Williams & Reid 2006; Brodie & Zuccarello 2006). Algal species are generally poorly known, with fewer described species compared to higher plant species. Species richness and the proportion of described to undescribed species varies among the algal phyla (Table 1). The diatoms, whose first representatives appeared in the fossil record circa 190 million years ago (Sims *et al.* 2006), are both the most speciose and poorly known phylum, with only approximately 4% of species described. The sister group of the diatoms, the Bolidiophyceae, comprises 3–5 species of small flagellates discovered during the last decade (Guillou *et al.* 1999). Among the seaweeds, the

red algae, an ancient lineage dating back to the oldest (1200 million years old) resolvable eukaryotic fossil *Bangiomorpha pubescens* Butterfield (2000) are the most speciose macroalgal phylum, with approximately 25% of species described by science.

This paper establishes the crucial role that marine phototrophs play in marine ecosystems and reviews the species-level knowledge base for these organisms in southeast Queensland, a region defined geographically from Noosa to Coolangatta in the tropical to temperate biogeographic overlap zone on the Australian east coast. For this region, species of marine cyanobacteria and algae are poorly known whereas seagrass and mangrove species are comparatively well known. The importance of detailed taxonomic, ecological and biogeographic data on the marine phototrophic species is discussed in relation to biotic surveys, biomonitoring, algal blooms, invasive exotic species, rare and threatened species and marine protected areas. Future research directions are outlined to collect much needed data on species composition, abundance, ecological and geographical distribution patterns of cyanobacterial and algal species in marine communities of SE Qld at varying spatial and temporal scales, highlighting the pressing need for rigorously-collected detailed data at the species level to underpin marine management and conservation planning.

SIGNIFICANCE OF MARINE PHOTOTROPHS

Phototrophs are of great ecological, conservation and economic importance in marine ecosystems, providing a wide range of essential 'ecosystem services' (Myers 1996; Costanza *et al.* 1997) that sustain ecosystem function, the human race, and the health of our planet. Considering only two ecosystem services, estuarine algal/seagrass beds are valued at $US19,004 ha^{-1} year^{-1} for the recycling of nutrients and raw materials (Costanza *et al.* 1997) and $US30,000 ha^{-1} year^{-1} in fishery production (Virnstein & Morris 2000). Loss of vital ecosystem services from estuaries degraded by coastal development and pollution costs the US more than $200 million year^{-1} in lost commercial fish production (Myers 1996). Marine phototrophs contribute significantly to numerous ecosystem services including primary production, habitat heterogeneity, biogeochemical cycling, biostabilisation of sediments, and are also useful as environmental indicators and sources of marine natural products.

1. PRIMARY PRODUCTION AND ENERGY FLOW IN MARINE FOOD WEBS

As primary producers, cyanobacteria, algae, seagrasses and mangroves underpin marine food webs in a biosphere where total global marine and terrestrial net primary production are similar (Field *et al.* 1998). Algae are the major marine primary producers in all marine ecosystems (Mann, 1973, 1988; Field *et al.* 1998). Phytoplankton support oceanic and coastal food webs (Mallin & Paerl 1994; Deegan & Garritt 1997; Falkowski *et al.* 1998; Calbet & Landry 2004). Algal turfs and symbiotic dinoflagellates in corals contribute about 50% and 30% of the primary production of healthy coral reef ecosystems respectively (Adey & Steneck 1985; Klumpp & McKinnon 1989; Adey 1998), with 60–100% of turf algal production consumed by the intense grazing pressure of herbivores (Adey & Steneck 1985; Adey & Goertemiller 1987; Klumpp & McKinnon 1989). Cyanobacterial and/or algal mats/biofilms adhering to muddy/sandy substrata are often the dominant primary producers in estuarine ecosystems (Underwood & Kromkamp 1999). Algal primary production (benthic microalgae, epiphytes, phytoplankton) in seagrasses communities often far exceeds seagrass primary production (Kitting *et al.* 1984; Daehnick *et al.* 1992; Mateo *et al.* 2006), with a large proportion (20–62%) of epiphyte primary production consumed by herbivores (Klumpp *et al.* 1992). Mangrove and seagrass communities are highly productive, but most production enters detrital food webs (Newel *et al.* 1995, Marguillier *et al.* 1997; Valentine & Duffy 2006), with low proportions (10–30%) of seagrass production removed by herbivores (Mateo *et al.* 2006; Valentine & Duffy 2006).

2. HABITAT HETEROGENEITY

Mangrove, seagrass, macroalgal and cyanobacterial species are 'foundation species' (Dayton 1972, 1975) or 'ecosystem engineers' (Jones *et al.* 1994), structuring the local environment to either positively or negatively affect the survival of other species in the community. Foundation species increase habitat heterogeneity and supply predator protection for many organisms, including juvenile stages of commercially-exploited fishery species (Brawley & Adey 1981; Kitting *et al.* 1984; Poore 1994; Haywood *et al.* 1995; Heck *et al.* 2003; Gillanders 2006). Seagrass, mangrove and kelp communities are widely acknowledged as foundation species but many other algal/cyanobacterial species also fulfil this important ecological role. For example, the green alga *Halimeda* and coralline red algae are 'ecosystem engineers' on coral reefs, with CO_3 sediments derived from these calcareous algae being quantitatively more important for coral reef construction than CO_3 sediments from corals (Stoddart 1969; Milliman 1974, Hillis-Colinvaux 1980; Drew 1983; Rees *et al.* 2007). Encrusting coralline red algae provide further ecosystem services by retarding reef erosion from high-energy oceanic waves by overgrowing, cementing and stabilising calcareous sediments on outer reef rims (Womersley & Bailey 1969; Littler & Doty 1975; Littler & Littler 1984; Adey 1998).

3. GLOBAL BIOGEOCHEMICAL CYCLES

Marine phototrophs are important in the global carbon cycle, removing CO_2 from atmospheric and oceanic sinks and sequestering some of C fixed by phytoplankton by sedimentation in the ocean depths (Raven & Falkowski 1999) and in CO_3 sediments in *Halimeda* biotherms on coral reefs (Rees *et al.* 2007). Phytoplankton,

particularly species forming massive oceanic blooms, and macroalgae play a central role in the global sulphur cycle, being the major source of atmospheric dimethyl sulphide, a compound which forms cloud condensation nuclei and cloud droplets to bioregulate climate by influencing the Earth's radiation budget (Charlson *et al*. 1987; Bates *et al*. 1992; Malin & Kirst 1997). Nitrogen-fixing cyanobacterial species are important in the global nitrogen cycle, potentially adding tons of N to marine ecosystems during blooms (Capone *et al*. 1997).

Algal and cyanobacterial mats are important in the regulation of the benthic-pelagic nutrient cycling loops (Lapointe & O'Connell 1989, Lavery & McComb 1991, Thybo-Christesen *et al*. 1993, Valiela *et al*. 1997, Sundback *et al*. 2003).

4. BIOSTABILISATION OF SEDIMENTS

Mangroves, seagrasses, algal and cyanobacterial mats stabilise unconsolidated sediments by reducing the erosive capability of seawater passing through/over these communities (Yallop *et al*. 1994; Underwood 1997; Paterson & Black 1999; Gacia & Duarte 2001; Saenger 2002; Kenworthy *et al*. 2006). Decreasing water velocity increases sedimentation of particulate matter, improving water clarity and reducing water column nutrient levels. Mangrove canopies also reduce wind velocities, thus protecting terrestrial vegetation and buildings during storms and cyclones.

5. INDICATORS OF ENVIRONMENTAL HEALTH

Decreases in seagrass depth ranges or in the areal extent of seagrass communities are used to monitor seagrass ecosystem health (Dennison & Abal 1999). Algal species respond quickly to environmental change with changes in species composition and abundance. Eutrophication usually results in decreased algal species richness, changes in species composition and community complexity (Littler & Murray 1975; Lapointe & O'Connell 1989; Brown *et al*. 1990; Hardy *et al*. 1993, Middelboe & Sand-Jensen 2000). Algal species intolerant to fluctuating salinities, elevated nutrient levels and toxic substances are replaced by fewer tolerant species which dramatically increase in abundance. Sensitivity of early developmental stages of algal species to low concentrations of toxicants is used by bioassays to assess water quality (Reed *et al*. 1994; Kevekordes 2001).

6. NATURAL PRODUCTS

Marine algae are used extensively for human and animal food and in industrial and medical products (Borowitzka & Borowitzka 1988; Lembi & Waaland 1988). In 2004, mariculture of *Laminaria japonica* (kombu), *Porphyra* (nori), and *Undaria pinnatifida* (wakame) produced 4.5, 1.4 and 2.5 million metric tons valued at 2.75, 1.34 and 1.02 billion US$ respectively (FAO 2006), being used primarily for human food. The red alga *Porphyra* is used as the outer wrapper in sushi. Hydrocolloids extracted from excess maricultured and wild-collected kelps (alginates) and red algae (agar, carrageenans) are used in the food processing industries. Antifouling agents added to marine paints have been extracted from algae (de Nuys & Steinberg 1999). Marine algae exhibiting antibacterial, agglutinin, antifungal, anticoagulant, antitumor and antiviral activity are potential sources of new bioactive chemicals, important for supplying new drugs to combat resistant infectious and newly emergent diseases.

KNOWLEDGE BASE

The biodiversity of mangrove and seagrass species of SE Queensland is well known. Eight mangrove species occur in sheltered bays and estuaries in the region (Hegerl & Timmins 1973; Shine *et al*. 1973; Dowling 1979, 1986; Davie 1984, 1992; Hyland & Bulter 1988), all of which are widely distributed in the tropical Indo-West Pacific. In SE Qld, *Avicennia marina* (Forssk.) Vierh. is the most ecologically widespread and abundant species with *Rhizophora stylosa* Griff. and *Aegiceras corniculatum* (L.) Blanco also common. *Lumnitzera racemosa* Willd. and *Excoecaria agallocha* L. reach their southern distribution limit in Moreton Bay (Macnae 1966). The mangrove fern *Acrostichum speciosum* Willd. is found in tidal creeks and swamps in the region. Hyland & Bulter (1988) surveyed the species composition and distribution of mangrove communities in SE Qld, which are best developed on the muddy deltas of the Logan, Pimpama and Coomera Rivers in southern Moreton Bay. These communities are unique being the largest area of mangroves on the east Australian coast south of the Wet Tropics region.

Eight species of seagrasses (including *Halophila minor* (Zoll.) Hartog, this volume) inhabit the

sheltered estuaries and bays of SE Qld (Young & Kirkman 1975; Kirkman 1975; Poiner 1985; Hyland *et al*. 1989; Poiner *et al*. 1992; Dennison & Abal 1999; McLennan & Sumpton 2005). With the exception of *Zostera capricorni* Asch. which is geographically limited to eastern Australia, New Guinea and New Zealand, the other species are widely distributed in the tropical Indo-West Pacific. Moreton Bay is the southern distribution limit of *Syringodium isoetifolium* (Asch.) Dandy, *Cymodocea serrulata* (R.Br.) Asch. ex Magnus and *Halodule uninervis* (Forssk.) Asch. (Poiner & Peterkin 1995). *Zostera capricorni* is the most abundant and widespread species in the region, frequently growing as monospecific meadows. The clear oceanic-influenced waters of eastern Moreton Bay support the most species-rich and abundant seagrass communities in the region, unlike western Moreton Bay where high turbidity limits seagrass growth (Young & Kirkman, 1975; Poiner, 1985; Abal & Dennison, 1996).

Our knowledge of the marine algal and cyanobacterial species of SE Qld is dismally incomplete, these species having received minimal taxonomic and ecological study. There are no comprehensive marine algal/cyanobacterial floras for the Australian east coast, and this represents a major impediment to including these organisms in ecological surveys, documenting biodiversity patterns or devising strategies for marine environmental management and conservation planning. Algal and cyanobacterial species are common on rocky shores, deep rocky reefs, sand and mud flats, and in seagrass and mangrove communities in SE Qld, but with the lack of adequate sampling or study, the identity of many local species may not be accurately known, and species richness and endemism may be underestimated.

Knowledge of the marine macroalgal (Chlorophyta, Phaeophyta, Rhodophyta) species of SE Qld is largely limited to eight scientific papers (Askenasy 1894; Johnston 1917; Cribb 1979; Saenger 1991; Phillips 1997b, 1998a, Phillips, 2002; Phillips & Price 1997) and references to various species scattered throughout the scientific literature. Based on vouchered herbarium specimens at the Queensland Herbarium (BRI), approx. 275 species have been collected from

Caloundra to Jumpinpin over the last 100 years (Phillips 1998a). While the BRI macroalgal collection is extremely valuable and indicates high macroalgal species richness for this poorly studied region, limitations of these data ensure that they are inadequate for the purposes of environmental management and conservation planning for the following reasons:

1. Specimens have been updated to currently accepted names, but with the exception of some brown algal species (Phillips & Price 1997), many species identifications have generally not been verified (though they could be with further taxonomic study). Thus the collection undoubtedly includes misidentified species, species whose concepts have changed following subsequent taxonomic revision, and species new to science. It is vital that herbarium specimens bear the correct species name as this establishes a species' biological identity and its ecological role. As Gotelli (2004) emphasises, correct identifications are crucial for reliable community analyses.

2. Specimens result from opportunistic and sporadic collecting over the last 100 years and not from surveys using standardised sampling effort. The number of species recorded at a locality is related to sampling effort (Womersley & Bailey 1970; Edgar *et al*. 1997; Middelboe *et al*. 1997; Bianchi & Morri 2000; Gotelli 2004). Therefore, comparisons of macroalgal species richness at different localities, or documenting macroalgal distribution patterns based on a highly variable sampling effort, are scientifically flawed. The most species rich localities, Caloundra (103 species) and Redcliffe (109 species), were sampled on many occasions and cannot be compared with sites sampled only once to record <10 species.

3. Specimens were not collected as part of a quantitative sampling program using standard ecological techniques and consequently there is no data on species abundance, community structure or on the spatial and temporal variability in macroalgal communities on annual, decadal or longer time scales. There is also little indication whether small, inconspicuous, subtidal, or seasonal macroalgal species were included in the collections. Furthermore, locality data from the many drift specimens is unreliable,

apparent from the Noosa collection of the temperate brown alga *Hormosira banksii* (Turner) Decne., which has a northern geographical distribution limit in northern NSW.

Current knowledge indicates that macroalgal species with tropical affinities predominate in Moreton Bay (65%), with cool temperate species ranging from southern Australia (15.2%) and species with cosmopolitan distribution patterns (20.8%) also contributing to the flora (Phillips 1998a). In SE Qld, macroalgal communities are best developed on rocky substrata on the Redcliffe Peninsula, on rocky headlands of the wave swept coasts (pers. observ.) and on deep water rocky outcrops east of Stradbroke and Moreton Islands (Stevens & Connolly 2005). In sheltered areas with muddy/sandy substrata, macroalgal species grow on firm substrata such as mollusc shells, rocks and pebbles and as epiphytes on mangrove roots and seagrasses.

Little is known of the biodiversity of marine phytoplankton of SE Qld despite these organisms fixing approx 60% of the total primary production of the Moreton Bay ecosystem (Eyre & McKee 2002). Currently, there is no phytoplankton species list and little data on the ecology of phytoplankton communities in SE Qld, but species richness is expected to far exceed that of the macroalgae. Phytoplankon communities are generally spatially variable, evident from domination by either tropical Coral Sea dinoflagellates particularly *Ceratium spp.* or the diatom *Paralia sulcata* (Ehrenberg) Cleve (as *Melosira sulcata* (Ehrenberg) Cleve) and the dinoflagellate *Dinophysis caudata* Saville-Kent in the oceanic and estuarine sections of Moreton Bay respectively (Ferguson-Wood 1964). Phytoplankton communities are generally composed of many different algal phyla. This is typified by a winter flood-influenced community in western Moreton Bay that comprised 145 species, including diatoms (81 species), dinoflagellates (54 species) and 1–2 species each of cryptophytes, chrysophytes, euglenophytes, prasinophytes and rhapidophytes (Heil *et al.* 1998a, b). The flood would be expected to shift phytoplankton species composition to more euryhaline species and consequently the lack of baseline monitoring data on species composition and abundance precludes interpretations of the

flood data collected during both a narrow sampling window and atypical prevailing environmental conditions. Phytoplankton blooms regularly occur in Moreton Bay but have not been documented in the scientific literature. The surf-zone diatom *Anaulus australis* Drebes et Schultz is recorded as blooming at Main Beach, Southport (Hewson *et al.* 2001) and more generally along SE Qld coasts (pers. observ.).

With the exception of *Lyngbya majuscula* (Dillwyn) Harv. and *Trichodesmium*, little is known of the marine cyanobacterial species of SE Qld. Cribb (1979) recorded 13 cyanobacterial species from salt marshes and mangroves in Moreton Bay, but this number gives little indication of cyanobacterial species richness for the region. Abundant thick mats of *Microcoleus chthonoplastes* Thur. ex Gomont, a species not previously recorded from Moreton Bay, are reported from areas of mangrove dieback at Whyte Island (Phillips & Kevekordes 2008).

Species richness or community structure of the microphytobenthos of Moreton Bay which is estimated to fix 85,000 t C year^{-1} (Eyre & McKee 2001) has not been documented. Microphytobenthos typically occurs as either microbial mats or biofilms on sandy/muddy substrata (Yallop *et al.* 1994). Stratified microbial mats are often mm thick, and are composed of three layers: an upper-most diatom mucopolysaccharide layer, a species-rich diatom midlayer, and a lower-most layer of filamentous cyanobacteria, often *Microcoleus chthonoplastes*, although species of *Oscillatoria, Spirulina, Merismopedia, Gloeothece, Lyngbya* and *Phormidium* may also be present. Biofilms are composed of many diatom species and diatom mucopolysaccharide and tend to be transient, relatively thin (100 μm) and unstratified. Microphytobenthic communities typically comprises 50 to 100 species at a locality (Underwood 1997, 2002; Underwood *et al.* 1998).

ISSUES

NEED FOR TAXONOMY

Taxonomic studies are urgently required to fully document biodiversity of marine cyanobacteria and algae of SE Qld by defining undescribed, under-described and inaccurately described species and compiling this data into

floras/field guides for the region. Taxonomy is the science that not only discovers and documents biodiversity (Wilson 2000, 2002) but also provides the biological reference system for recognising and naming species. The southern Australian marine macroalgal flora has been well documented, most recently in the six volumes of the 'Marine Benthic Flora of Southern Australia' (Womersley 1984, 1987, 1994, 1996, 1998, 2003) which has enabled these species to be included in many ecological and conservation studies, including analyses of the patterns of species richness and endemism (Phillips 2001). It is difficult to study or conserve species that can not be identified with certainty (Dayton 2003; Mace 2004). Species are unique entities, conveyed by the species name which is not an arbitrary concept, but a summary of the morphological, ultrastructural, physiological, biochemical, ecological, geographical and phylogenetic characteristics of the entity.

Our inability to recognise species has important implications for environmental and conservation management, clearly demonstrating that these strategies are as effective as the reliability of the taxonomy on which they are based (Knowlton *et al.* 1992; Knowlton & Jackson 1994; National Research Council 1995; Wilson 2000; Knowlton 2001; Womersley 2006). Environmental and conservation management must be underpinned by taxonomic precision and accuracy. Identifying constituent species is the key to understanding community structure and function, and for detecting the early warning signals of environmental change before large scale environmental degradation and massive species loss become apparent (National Research Council 1995; Dayton 2003). How can we effectively manage or conserve the many species we cannot recognise? This is particularly pertinent for many widely distributed cosmopolitan or pantropical marine 'species' now known to be 'species complexes' comprising two or more, often endemic, superficially similar sibling or cryptic species (National Research Council 1995). Prevalence of cryptic marine species has ensured that not only has marine biodiversity been underestimated (eg actual invertebrate species richness is three to five times higher than previously recognised for well studied coral reef

communities (see Knowlton & Jackson 1994 for review)) but also marine species generally have been erroneously thought to be common and widely distributed, two features thought to protect species from extinction (Roberts & Hawkins 1999). Many cryptic marine macroalgal species with restricted geographical ranges have been identified, necessitating the description of new genera (Phillips 1997a; Nelson *et al.* 2006) and new species (Phillips & Nelson 1998; Zuccarello & West 2003, 2006; Nelson *et al.* 2006; Zuccarello *et al.* 2006; Verbruggen *et al.* 2006). New conservation strategies will have to be developed for the marine biota that has more geographically restricted species than previously thought.

QUANTITATIVE BIOTIC SURVEYS

Biotic surveys are urgently required to address the complete lack quantitative data on the marine algae/cyanobacterial communities of SE Qld. These data are important for environmental management and conservation planning. It is expected that these assemblages will be spatially variable, occurring in different habitats such as the red algal *Bostrychia/Caloglossa* association characteristic of mangroves and also that seemingly similar habitats will have differing algal/cyanobacterial assemblages. These assemblages will also exhibit considerable temporal variability on seasonal, annual, decadal and longer term time scales in response to environmental variables. Ecological processes affecting algal/cyanobacterial community structure are complex and long term baseline datasets are required to separate natural variability from anthropogenic impacts, and to determine the effects of slow processes (eg global warming), episodic phenomena and high annual variability (Hawkins & Hartnoll 1983; Dayton & Tegner 1984; Southward 1991, 1995; Barry *et al.* 1995; Lewis 1996; Hiscock *et al.* 2003; Thibaut *et al.* 2005).

BIOMONITORING

Biomonitoring provides accurate appraisals of ecosystem health by sampling the biota which reflect the summation of all environmental variables over spatial and temporal scales rather than those variables present during sampling or being studied (Baldwin & Kramer 1994; Abel 1996). Currently, physico-chemical parameters

are monitored in SE Qld estuaries but these, even when monitored at frequent intervals, often fail to detect the delivery of episodic pulses of biologically-significant often peak concentrations of pollutants and nutrients into ecosystems. This is well illustrated by seasonal macroalgal blooms which inhabit apparently oligotrophic (nutrient-poor) waters (Lapointe & O'Connell 1989; Thybo-Christesen et al. 1993; Peckol et al. 1994), the result of bloom-forming algae absorbing high levels of spatially and temporally variable pulses of water column nutrients within hours or days (Kiirikki & Blomester 1996; Fong et al. 1993a, b; Kamer et al. 2001).

Seagrass depth ranges are currently used for monitoring water quality in Moreton Bay (Dennison & Abal 1999), a technique based on declines in many Australian seagrass communities attributed to decreased submarine light penetration from increased water turbidity or epiphyte growth (Bulthuis 1983; Cambridge & Mc Comb 1984; Cambridge et al. 1986; Abal & Dennison 1996). However, seagrasses occupy <5% of the area of Moreton Bay leaving an urgent need for a more widely applicable bio-monitoring system for the bay.

Algal and cyanobacterial species are valuable indicators of ecosystem health (both pristine and degraded ecosystems), responding quickly to anthropogenic-induced changes to the marine/estuarine environments with changes in species composition and abundances in these communities. Marked shifts in dominance from slow-growing perennial macroalgal species of healthy ecosystems initially to smaller frondose algae and then finally to fast-growing filamentous 'nuisance' macroalgal species are early warning signals of increasing nutrient enrichment, triggers to reduce high nutrient loading into aquatic systems long before eutrophication results in catastrophic algal blooms (Littler & Murray 1975; Valiela et al. 1997; Örnólfsdóttir et al. 2004).

ALGAL BLOOMS

The ongoing and worsening problem of coastal eutrophication has resulted in the increased frequency and intensity of algal blooms worldwide (Hallegraeff 1993; Chrétiennot-Dinet 2001). Management strategies to ameliorate decadal long macroalgal blooms aim to reduce high N

and P loadings into eutrophic estuaries by 30–80% (Jorgensen & Richardson 1996; Boesch et al. 2001; Paerl et al. 2003). Knowledge of the biology and ecology of bloom-forming species is also necessary in order to understand why these species cause shifts in species composition in communities and maintain prolonged competitive dominance (Valiela et al. 1997; Smayda 1997; Millie et al. 1999).

Transient algal and cyanobacterial blooms which regularly occur in SE Qld coastal waters can be expected to become more common with the increasing human population in the region. Species of the 'green tide' genera *Cladophora*, and *Ulva* (which now includes *Enteromorpha*) and phytoplankton (such as *Heterosigma akashiwo* (Hada) ex Sournia, *Prorocentrum micans* Ehrenberg, *Scrippsiella trochoidea* (Stein) Balech ex Loeblich III) commonly form blooms in the region, but it is the cyanobacterial species *Lyngbya majuscula* and *Trichodesmium* and the brown alga *Hincksia sordida* (Harvey) Silva which have had the greatest impact in SE Qld. Periodic, short lived (eg days) blooms of the tropical planktonic *Trichodesmium* (often commonly and erroneously referred to as 'coral spawn') are transported into coastal waters in SE Qld and many localities to Tasmania by the southward flowing East Australian Current (Ajani et al. 2001).

Recurrent nuisance blooms of *Lyngbya majuscula* have been apparently restricted in Moreton Bay to the eastern banks, Deception Bay and Pumicestone Passage. The supply of either or both N and P control peak rates of primary production of bloom-forming species in estuaries (Valiela et al. 1997). However, *Lyngbya majuscula* bypasses N limitation by fixing N_2 in the dark (Lundgren et al. 2003; Elmetri & Bell 2004), and not in the light (Dennison et al. 1999) when oxygen-labile nitrogenase is degraded during photosynthesis.

The macronutrients N and P have the greatest potential to constrain algal/cyanobacterial growth (Cloern 2001; Twomey & Thompson 2001; Miao et al. 2006). If the micronutrient Fe limits the growth of *Lyngbya majuscula* in Moreton Bay (Dennison et al. 1999), P would have to be in excess, contrary to studies which report both the Bay (Eyre & McKee 2002) and

growth of Moreton Bay *Lyngbya majuscula* (Elmetri & Bell 2004) to be PO_4 limited. Clearly, Fe limits cyanobacterial/algal growth in high nutrient/low chlorophyll remote oceanic regions (Coale *et al*. 1996; Behrenfeld & Kolber 1999), where Fe can not be recycled from the ocean depths and is quickly depleted from surface waters unless replenished by the atmospheric transport of terrestrial aeolian dust (Duce & Tindale 1991; Zhaung *et al*. 1999). In contrast to these oceanic regions, Moreton Bay has high chlorophyll levels, the sediments are Fe-rich (Preda & Cox 2002) and there should be sufficient bioavailable Fe^{2+} from organic material supplied by riverine inputs (Johnson *et al*. 1999; Wetz *et al*. 2006, Tovar-Sanchez *et al*. 2006). Further-more, ambient seawater NO_3 levels >2.5 µM common in Moreton Bay would inhibit the energetically-expensive N fixation in *Lyngbya majuscula*, similar to the inhibition demon-strated in *Trichodesmium* (Mulholland *et al*. 2001; Holl & Montoya 2005), thus reducing the Fe requirement for nitrogenase and associated metabolic pathways (Howarth *et al*. 1988; Paerl 1990). This would also be a plausible expla-nation for the low rates of N_2 fixation reported for Moreton Bay *Lyngbya majuscula* by Watkinson *et al*. (2005).

During the spring/early summer of 2002 to 2005, *Hincksia sordida* bloomed in the Noosa River estuary and at Main Beach, Noosa, greatly affecting the recreational use of the popular swimming beach (Phillips 2006). During blooms, bulldozers removed the decomposing algal masses fouling the beach, but large amounts remained suspended in the surf. *Hincksia sordida* is an estuarine alga, reported to grow to one metre in length in sheltered Moreton and Port Phillip Bays. The source of the massive injections of nutrients into the Noosa River system and Laguna Bay need to be identified and reduced in order to prevent future blooms in the area.

EXPECTED EFFECTS OF CLIMATE CHANGE

Average global surface temperature has increased during the generalised warming trend of the last 150 years. Sea surface temperature (SST) which is projected to rise by 2-3 °C around the Australian continent by 2070 may potentially affect the physiology, phenology

and geographical distribution of marine species (Hughes 2000). Relatively small changes in temperature have already affected marine species (Barry *et al*. 1995; Southward *et al*. 1995; Sagarin *et al*. 1999), including dramatic declines in the kelp forests on the Tasmanian east coast (Edyvane 2003), but there is little understanding of the effects on the marine biota of larger increases in SSTs. We do know that during the Quaternary warming episodes, terrestrial plant species responded independently and not as a community moving at different rates and in different directions during climate-induced latitudinal shifts in geographical range (Davis & Bodkin 1985; Overpeck *et al*. 1991; Jackson & Overpeck 2000; Hannah *et al*. 2005). Conse-quently, novel species associations were created which may have dramatically altered species interactions that organised and structured communities.

Changing climate could affect the marine phototrophs of SE Qld, with many species at or near either their southern or northern distribution limits in this tropical to temperate biogeographic overlap zone. Range expansions of tropical species and range contractions of temperate species would potentially alter species composition of marine plant/algal communities and, particularly when foundation species are involved, will impact on marine community structure. Knowledge of the physiology, phen-ology and the geographical ranges is urgently required to predict the response of marine phototrophs to climate change. Furthermore, extinctions may occur when migrating species are deprived of suitable habitat.

EXOTIC SPECIES

Biological invasions threaten the integrity and function of recipient ecosystems. Human mediated transport of exotic marine species across their natural dispersal barriers has probably occurred for centuries (Adams 1983; Ribera & Boudouresque 1995), with only a small proportion of introduced species be-coming invasive. According to the 'tens rule', the probability of an introduced species becoming established in the wild and then for an established species to become invasive is on average 10 % for each transition (Williamson & Fitter 1996a, b). Two invasive seagrass species

are known: *Zostera japonica* Asch. & Graebner and *Halophila stipulacea* (Forssk.) Asch., invaders of the North American Pacific Coast and Mediterranean Sea respectively (Ribera & Boudouresque 1995; Kenworthy *et al.* 2006). In contrast, many macroalgal and phytoplankton species have invaded marine ecosystems worldwide (Hallegraeff 1993; Ribera & Boudouresque 1995).

Detecting the presence of exotic marine algal species in Moreton Bay is not straightforward, requiring knowledge of the presence and bio-geographical ranges of native species resident within the ecosystem as well as the regular monitoring of species composition to detect newly-arrived exotic species (Valentine & Jablonski 1993; Jackson 1994). Biotic surveys of shipping ports, marinas and adjacent areas, often entry points for exotic marine species, are best undertaken by teams of taxonomic experts capable of identifying exotic species, including invasive cryptic species misidentified as their native congeners (Gavio & Fredericq 2002; Cohen *et al.* 2005; Thomsen *et al.* 2005; Arenas *et al.* 2006).

The pressing need for detailed species-level taxonomic and ecological information to iden-tify putative introduced species is well illus-trated by the *Caulerpa taxifolia* (Vahl) C.Agardh and *Pfiesteria* scenarios. Well known since the 1980s as a Mediterranean invader (Meinesz & Hesse 1991), the green macroalga *C. taxifolia* is indigenous to tropical/subtropical Australia (Phillips & Price 2002), and a common inhabi-tant of Moreton Bay seagrass communities (Young & Kirkman 1975). This refutes the suggestion of Pillen *et al.* (1998) that exotic *C. taxifolia* was invading Moreton Bay. Reports of introductions of the toxic dinoflagellate *Pseudo-pfiesteria shumwayae* (Glasgow et Burkholder) Litaker, Steidinger, Mason, Shields et Tester (as *Pfiesteria shumwayae* Glasgow et Burkholder) into Australian estuaries identified only by 'species-specific' PCR probes applied to environ-mental samples are now considered erroneous (Park *et al.* 2007a, b). Monitoring of Australian estuaries failed to find the species and sub-sequent studies with rDNA *Pseudopfiesteria shumwayae*-specific primers produced 'false-positive' reactions with the dinoflagellate

Cryptoperidiniopsis brodyi Steidinger et Litaker, suggesting that the latter species common in Australian estuaries had previously been mis-identified as *Pseudopfiesteria shumwayae*.

RARE AND THREATENED SPECIES

Rare species generally have restricted geo-graphical ranges, specific habitat requirements and small population size (Rabinowitz *et al.* 1986). Rarity is considered to be one factor which could determine the extinction risk of a species (Gaston 1996). Threatened species are assigned to various categories: critically en-dangered, endangered, vulnerable or rare (IUCN 1994). In contrast to terrestrial species, marine species have only been recently recog-nised as 'at risk of extinction', largely due to insufficient data available on geographical range, habitat specificity and minimum viable population size which determine the conser-vation status of these species (Phillips 1998b). Many marine species are now known to have restricted geographical ranges (Roberts & Hawkins 1999; Knowlton 2001; Roberts *et al.* 2002) and declining populations, largely deci-mated by habitat degradation and loss.

With further research, rare and threatened SE Qld species will be identified as requiring protection, similar to many marine macroalgal species afforded protection in other areas of the world. These include vulnerable rapidly decli-ning endemic Mediterranean species of the brown algal genera *Cystoseira* and *Sargassum* (Ballesteros *et al.* 1998; Boudouresque *et al.* 2005; Thiery *et al.* 2005), 15 rare Canadian marine macroalgal species (Hawkes 1991) and 27 threatened macroalgal species from the Wadden Sea (Nielsen *et al.* 1996). Conservation of British macroalgae has progressed from 40 species targeted for priority conservation (John & Brodie 1996) to approximately 260 species on a working list of 'rare' species (Brodie *et al.* 2005). The seagrasses *Enhalus acoroides* (L.f) Royle, *Halophila johnsonii* Eiseman in Eiseman et McMillan, *Halophila decipiens* Ostenf., *Zostera asiatica* Miki and *Zostera caulescens* Miki are listed as rare or threatened species on other continents (Kenworthy *et al.* 2006).

Knowledge of species abundances and distri-butions are required to determine extinction risk. In addition, rare species are often difficult

to survey and identify and relatively little tends to be known of their ecology. There are rare endemic macroalgal species in the SE Qld flora such as the brown alga *Tomaculopsis herbertiana* Cribb known only from Caloundra and Byron Bay. Other local macroalgal species are obviously at risk, particularly species of the Dasycladales which are habitat specialists, typically growing in shallow estuaries, which are often the sites of human-mediated disturbance and habitat destruction.

PROTECTING MARINE BIODIVERSITY

Increasing pollution and habitat destruction caused by the rapidly increasing human population of SE Qld threatens to destroy the marine biodiversity of the region unless substantial efforts are directed towards protecting the biota. Marine Protected Areas (MPAs) such as the Moreton Bay Marine Park (MBMP) are zoned as multi-purpose areas to fulfil various social, economic, regional and pragmatic criteria (Ballantine 1991; Salm & Price 1994), ranging from recreation zones to fisheries management areas to preservation zones with strict protection (Gubbay 1995). Only preservation or 'no take' zones carefully defined with respect to location, size and the comprehensive and adequate representation of species, habitats and ecosystems will adequately protect biodiversity (McNeill 1994; Kelleher *et al*. 1995; Agardy 1995, 2000; Jameson *et al*. 2002; Lubchenco *et al*. 2003). However, few MPAs including the MBMP have been designed with sufficient scientific input to achieve appropriate boundaries and sizes (Jameson *et al*. 2002). In the absence of biotic data, the frequently-used easily-measured cost-effective abiotic surrogates are inadequate compared to local-scale rigorous biological surveys and habitat mapping for zoning MPAs (Edgar *et al*. 1997; Stevens & Connolly 2004).

Current zoning of MBMP aims to protect 'iconic' species (dugongs, turtles) and high profile marine habitats as coral reefs, mangroves and seagrass beds (Annon. 1997). These habitat types account for <10% of the MPA area (Stevens & Connolly 2005), protecting areas perceived to have high value rather than protecting a full range of habitats representative of the biodiversity in the MPA. As < 1% of the MBMP is currently zoned as 'no take' zone, which equates to the full protection given to

terrestrial national parks, the current rezoning planning needs to follow international best practise in MPA management (National Research Council 2000; Roberts & Hawkins 2000; Roberts *et al*. 2003) and designate 'no take' zones of 30–50 % of the MBMP area including all habitat types if we are to make serious attempts to conserve the marine biodiversity of SE Qld. This benchmark has already been set by the recent rezoning of Great Barrier Reef Marine Park where the network of 'no-take' areas increased to at least 20% of all 'bioregions' in the park and 33% of the overall MPA area (Fernandes *et al*. 2005). The Final Zoning Plan for MBMP must also outline the adaptive management strategies with clearly defined goals, measurable outcomes, and rigorous biotic sampling and data analyses in order to determine whether the management is effectively protecting biodiversity.

The scientific rigor gained from local scale habitat mapping and habitat classification schemes are prerequisites for delimiting ecological boundaries necessary for defining representative areas for MPA planning (Stevens 2002). An inclusive approach using subtidal transects on an almost bay-wide scale (Stevens & Connolly 2005) provided a quantum leap forward in the knowledge base on the extent and distribution of habitat types in MBMP rather than the rehash of previously published incomplete data largely on iconic groups reproduced in a large number of reports (eg Brisbane River Management Group, 1996, Dennison & Abal 1999). Stevens & Connolly (2005) documented previously unknown habitats, including deep water algal reefs, and discovered previously unrecorded seagrass meadows. While video-recording permits the collection of much cost effective data and has immense value in mapping habitat extent and type, the next logical step is to determine the species composition and abundance of all biota occurring in the habitat types. Monitoring using rigorous sampling and analyses is crucial to determine the present status of species (how many? where? increasing or decreasing?) in order to determine if the management strategies for the MBMP are effectively conserving biodiversity. It should be remembered that not all habitats of the same type have a similar species composition, evident

from the sponge fauna of 10 Sunshine Coast reefs, which recorded 34% species endemism per reef and 60% of the 247 species as rare (Hooper & Kennedy 2002). Important questions to be evaluated if MPAs are to protect biodiversity include whether MPAs preserve the largest possible number of species, including endemic species and whether the surviving habitat fragments are large enough to sustain populations indefinitely.

FUTURE RESEARCH DIRECTIONS

Conservation biology relies heavily on detailed knowledge of the interconnected fields of taxonomy, systematics, ecology, and biogeography (Clarke 1992; Carlton 1993; National Research Council 1995), and endeavours to maintain and protect biodiversity (including little understood and overlooked species) at all spatial scales (Clarke & May 2002; Kenworthy *et al.* 2006). I have outlined a number of knowledge gaps that hamper the development of effective environmental management and conservation strategies for marine algae and cyanobacteria of SE Qld. These are summarised below, along with recommended research directions.

1. Studies on taxonomy and systematics using both traditional (morphology, anatomy, breeding barriers etc) and molecular methods are urgently required to establish well defined taxonomic boundaries for described species, identify cryptic species, and describe species new to science. This new information should be collated into algal/cyanobacterial field guides and floras to facilitate accurate species identification necessary to include these species in ecological studies and in environmental and conservation management strategies.

2. Considerable efforts should be directed towards developing and undertaking a well designed rigorous program of quantitative surveys documenting species composition and abundance. This will allow a better understanding of the structure of marine algal/cyanobacterial communities of SE Qld. Such a sampling program needs to be conducted over long time scales, as the 'short termism' of most ecological surveys (a year or less) can neither document the spatial and temporal changes caused by the complex ecological processes affecting community structure (Lewis 1996;

Bianchi & Morri 2000; Hiscock *et al.* 2003), nor separate natural variability (effects of slow processes, episodic phenomena, high annual variability) from anthropogenic impacts (Southward 1991; Hiscock *et al.* 2003; Thibaut *et al.* 2005).

3. Important areas for algal/cyanobacterial conservation need to be identified and designated in the SE Qld region. Areas of high conservation significance are defined as those containing outstanding assemblages of rare, threatened, vulnerable and/or endemic species, or an exceptionally rich flora, or an outstanding example of a habitat type of known algal/cyanobacterial importance.

4. Greater attention should be paid to determining whether environmental management policies are successful, development is truly sustainable, and areas of high conservation significance are adequately protected. Environmental management and conservation planning decisions must be based on scientific data gained from monitoring programs determining the ongoing status of species and communities (Bourdouresque *et al.* 1995; Bianchi & Morri 2000). For example, the detection of many local population losses may be the early warning signal necessary to avert a species' path to global extinction (Ehrlich & Daily 1993). Extinction is irreversible, once a species has become extinct there are no management or conservation strategies which can restore that species.

5. The human race, including those living in SE Qld, needs to accept the challenge to reduce the current unprecedented global loss of biodiversity, projected to be two-thirds of all species by the end of this century (Raven 2002). We need to preserve and manage natural ecosystems in the face of escalating anthropogenic threats before these systems collapse and can no longer provide us with the resources and services on which we depend. We are the custodians of the planet, and unless we act now to preserve biodiversity, we will be judged harshly by future generations.

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Long-term changes in aquatic vegetation associated with structural modification and altered hydrology in a subtropical east Australian estuary

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ABSTRACT

A *Zostera capricorni* community is formally recorded for the first time in Currumbin Creek on the subtropical east Australian coast. The seagrass community extends approx. 2 km along both sides of the creek just below low tide mark, growing either in patches of variable size or more commonly as broad bands up to 5 m in breadth. The community consists of dense subtidal *Zostera capricorni* plants growing with subtidal *Halophila ovalis*. Leaves of *Zostera capricorni* were typically up to 70 cm long, considerably longer than previously reported for the large growth form of the species. Biological surveys undertaken over the last two decades had reported seagrasses as absent from Currumbin Creek. However, a forgotten consultancy report documented the loss of a small *Zostera capricorni* community in the creek following large-scale dredging of the internal delta in 1974. It is unlikely that seagrasses would have recolonised Currumbin Creek until after the cessation of sand dredging in 1992. Recent extension of the seagrass community much further upstream than previously reported is consistent with the change to marine conditions following training wall construction in 1973 which maintains the creek mouth permanently open to the sea. Previously, lower Currumbin Creek had oscillated between a prolonged freshwater phase when accumulated sand isolated the creek from the sea and a shorter marine phase that followed episodic high runoff events when the flooded creek cut a new entrance to the sea. Lessening of the freshwater influence has produced environmental conditions more conducive to seagrass growth and has also led to the replacement of freshwater riparian vegetation with mangroves. Seagrasses are a valuable resource in coastal marine ecosystems and it is essential to develop management strategies to ensure the survival of the Currumbin Creek seagrass community. ❑ *Zostera capricorni, Halophila ovalis*, expanding seagrass community, habitat modification, sand dredging, Currumbin Creek, Australia.

Negative impacts of increasing population and coastal development on the biota and ecosystem integrity of coastal southern Queensland have long been recognised (Coaldrake 1961; Saenger & McIvor 1975; Thompson 1975; Co-Ordinator-General 1975; Hyland & Butler 1988; Hyland *et al.* 1989). The 200 km stretch of coastline from Noosa (26°23'S, 153°06'E) to Coolangatta (28°10'S, 153°33'E) on the Queensland/New South Wales border, known as the 'Sunshine Coast' to the north and the 'Gold Coast' to the south of Brisbane (27°28'S, 153°01'E),
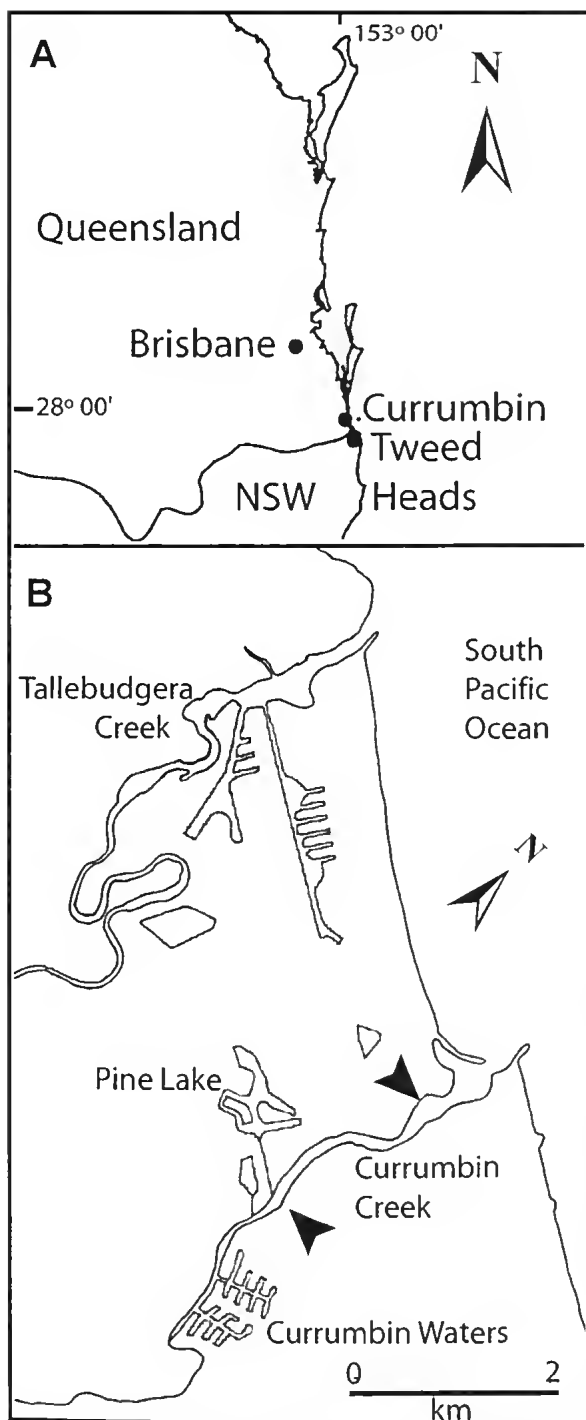
FIG. 1. Maps of Currumbin Creek, SE Queensland, Australia. **A**, location in relation to Brisbane and the Gold Coast. **B**, showing the extent of the *Zostera* community marked by arrowheads; the downstream limit is close to the creek mouth and the upstream limit is near the outlet to Pine Lake.

has been popular as a recreational destination since the 1950s and as a residential area for the last 3 decades. This coastal development has resulted in the large scale loss of the terrestrial heath ecosystem (the wallum), the draining of wetlands and the modification of estuaries. By 1975, residential canal developments had been constructed on 8 of the 14 major estuaries within 130 km of Brisbane resulting in the loss of large areas of saltmarsh and mangroves (Saenger & McIvor 1975). Currently, an urban strip extends along the southern Queensland coast from Noosa to Coolangatta.

With the exception of Moreton Bay, little is known of the aquatic biota of southern Queensland estuaries. There have been no systematic biotic surveys which have monitored the estuarine species of the region. Compared to many other regions of the world, the few biological surveys of southeast Queensland estuaries are relatively recent, first undertaken by conservationists from the Queensland Littoral Society (Lewis & Ellway 1971; Ellway & Hegerl 1972; Hegerl & Timmins 1973; Shine *et al.* 1973) in order to document a biota threatened by habitat destruction from real estate and other developments. Other data on estuarine organisms in the Gold Coast region exists in reports by consultancy companies (Consultancy Study Group 1974; Saenger & McIvor 1975; Hollingsworth 1975; WBM Oceanics 2000) and Queensland Government departments, the latter including the Coastal Management Investigation for southern Queensland (Co-Ordinator-General's Department 1975) and surveys of mangrove (Hyland & Butler 1988) and seagrass communities (Hyland *et al.* 1989). However, retrieving data from consultancy and government reports is often difficult, as these reports are held by few libraries, are not indexed in scientific databases and are often forgotten with the passage of time. Major gaps in our knowledge base of species inhabiting southern Queensland estuaries still exist and the new data generated from current studies need to be stored in the widely accessible scientific literature.

Seven species of seagrasses are recorded for southern Queensland (Young & Kirkman 1975; Poiner 1984; Hyland *et al.* 1989) and an eighth species is newly recorded in this volume (Phillips *et al.* 2008). *Zostera capricorni* Aschers. is widely

distributed in sheltered bays, coastal lagoons and estuaries along the east Australian coast, growing intertidally and/or subtidally, often in a monospecific community or with *Halophila ovalis* (R.Br.) Hook f. In Moreton Bay, *Halophila spinulosa* (R.Br.) Aschers. and *Halophila decipiens* Ostenf. are usually subtidal species and *Halolude uninervis* (Forsk.) Aschers. frequently grows on sandy substrata. *Cymodocea serrulata* (R.Br.) Aschers. and *Syringodium isoetifolium* Aschers. are largely confined to the eastern oceanic influenced waters of Moreton Bay (Young & Kirkman 1975; Poiner 1984).

Previous surveys had reported Currumbin Creek on the subtropical east Australian coast (Fig. 1) to be devoid of seagrasses (Hyland *et al.* 1989; WBM Oceanics 2000). This paper reports the discovery of an extensive, dense, subtidal *Zostera capricorni* meadow in lower Currumbin Creek during a biotic survey undertaken in 2003 by GHD Pty. Ltd. for the Gold Coast City Council. The Currumbin Creek *Zostera* community comprises plants with considerably longer leaves (to 70 cm long) than the large growth form of the species reported from nearby Moreton Bay. A consultancy report has been located documenting the presence of a small seagrass community near the mouth of Currumbin Creek in 1974. The factors which presumably have facilitated the recent recolonisation and expansion of the current Currumbin Creek seagrass community are discussed.

METHODS

STUDY AREA

Currumbin Creek drains a narrow steep sided valley and flows into the South Pacific Ocean. Rainfall is highly seasonal and freshwater run-off from the Creek is markedly variable both seasonally and annually. The entrance of Currumbin Creek is kept permanently open to the sea and consequently lower Currumbin Creek functions as a tidal inlet (Consultancy Study Group 1974; D'Agata & McGrath 2002). The sandy substratum in the lower Currumbin Creek grades to mud approximately 2 km upstream from the entrance. The Pacific Highway bridges were constructed across Currumbin Creek in 1973/74 and two residential canal developments are located in the upper estuary.

PRESENCE AND EXTENT OF SEAGRASSES AND MANGROVES

Currumbin Creek estuary was surveyed by boat during a 0.11 m low tide on 11th October 2003. Seagrass distribution in the estuary was surveyed visually, recording distribution limits of the community. The extent, species composition and structure of the mangrove communities along the creek were also recorded.

Extensive searches of the scientific literature, consultancy and government reports, the Queensland Herbarium Database (HERBRECS), aerial photographs and historical photographic collections from libraries were undertaken in order to determine whether seagrasses grew in Currumbin Creek prior to or at any time since the commencement of large scale human development in the area in the 1950s. Presence and distribution patterns of mangrove communities fringing Currumbin Creek were also investigated as these communities are more frequently included in vegetation surveys, are easily visualised in historical and aerial photographs and are indicative of the brackish conditions suitable for seagrass growth.

RESULTS

Zostera capricorni grew in lower Currumbin estuary either as patches or as dense broad bands 1–5 m wide, parallel to the creek banks at depths of 0.5–1 m below low water level of the spring tides. No *Zostera capricorni* was found growing in the intertidal zone. The community extended from an upstream distribution limit at the outlet of Pine Lake on the northern creek bank, for approximately 2 km down both sides of the creek to just upstream of the Gold Coast Highway bridge (Fig. 1). The upper estuarine distribution limit of *Zostera capricorni* appeared to coincide with a change from sand/muddy sand to mud substrata, but this may be related more to turbidity as *Zostera capricorni* grows extensively on intertidal muddy substrata throughout Moreton Bay.

Leaves of *Zostera capricorni* grew to a maximum length of 70 cm, positioning the upper leaf blades in the well illuminated surface waters and permitting the extent of the *Zostera* community to be observed from above the water surface. The *Zostera* plants appeared healthy and actively growing with only small numbers

FIG. 2. **A**, Currumbin Creek, 1911, view looking upstream from Granny Birch's Island in the creek mouth (washed away by the 1931 floods), showing dense stands of *Melaleuca* along the creek banks and the lack of mangrove vegetation characteristic of tidal waters. (Image courtesy of the John Oxley Library). **B**, Currumbin Creek, 1904, view of the creek mouth looking north to Burleigh Headland, showing *Melaleuca* sp. growing on the northern creek bank on which mangroves now grow. (Image courtesy of the Gold Coast City Council Local Studies Library).

of algal epiphytes colonising the mature and senescing leaves. *Halophila ovalis* was observed to grow amongst *Z. capricorni* near the Pine Lake outlet as plants were inadvertently pulled free of the substratum when collecting specimens of *Zostera*. Destructive sampling would have been required to document the ecological distribution of the small *H. ovalis* plants growing in the turbid conditions in Currumbin Creek.

Avicennia marina (Forssk.) Vierh. (the grey or white mangrove) grew as broad continuous dense bands along both banks of Currumbin estuary to approximately 5 km upstream from the mouth. In the lower estuary, a few trees of *Rhizophora stylosa* Griff. (spotted or spotted-leaved red mangrove) grew on the seaward edge of the *Avicennia marina* community. Recruitment by many *Avicennia* seedlings was observed at several sites along the estuary.

There are no specimens of seagrass, collected *in situ* from Currumbin Creek, lodged in Queensland Herbarium (A. Bolin, Collections manager, HERBRECS database, Queensland Herbarium, pers. comm.). No published papers documenting the presence of seagrasses in Currumbin Creek were found from searching scientific databases, but the Libraries Australia catalogue listed consultancy reports recording seagrasses in Currumbin Creek in the early 1970s (Consultancy Study Group 1974; Hollingsworth 1975). In 1974, extensive beds of *Zostera capricorni* grew on protected sandbars on the northern bank inside the creek mouth, but this population was lost in 1975 following the destruction of the seagrass habitat from sand dredging.

Although not providing any information on the presence/absence of seagrass in the estuary, historical and aerial photographs of Currumbin Creek documented changes in the riparian vegetation along the creek from paperbarks (*Melaleuca* spp.) in the early 1900s to the appearance of mangroves in the 1950s (Figs 2A, B, 3). Between the 1950s and the 1970s, a mangrove community up to 80 m wide and comprising *Avicennia marina* trees to 5 m in height was restricted to the northern Creek bank near the creek mouth (Consultancy Study Group 1974; Hollingsworth 1975) (Fig. 3). Aerial photographs taken prior to 1970 also show the mouth of Currumbin Creek was

unstable, migrating northwards during the extended periods of low freshwater runoff when sand, deposited by the longshore transportation and littoral drift, progressively sealed off the creek from the sea (Fig. 3). During floods, the creek cut a new entrance to the sea along the southern creek bank.

DISCUSSION

The discovery of an extensive *Zostera capricorni* community in Currumbin Creek was unexpected as previous surveys of the estuary had not reported seagrasses (Cambridge *et al.* 1974; Hyland *et al.* 1989; WBM Oceanics 2000), even though seagrasses grow in Tallebudgera Creek (Lewis & Ellway 1971; Shine *et al.* 1973; Hyland *et al.* 1989) and the Tweed River (Ellway & Hegerl 1972), estuaries within 10 km to the north and south of Currumbin Creek respectively. The dense subtidal seagrass community in Currumbin Creek contrasts markedly with the seagrass community in nearby Tallebudgera Creek, where *Zostera capricorni* occurs in small isolated patches in both the intertidal (Lewis & Ellway 1971; Shine *et al.* 1973; Hyland *et al.* 1989) and subtidal zones (Lewis & Ellway 1971). *Halophila ovalis* has not previously been recorded from Currumbin Creek and the species is not known to occur in Tallebudgera Creek.

Leaves of *Zostera capricorni* from Currumbin Creek are considerably longer than the 7–50 cm length range (den Hartog 1970; Poiner 1984) previously reported for the species. The larger leaf size in *Zostera capricorni* is attributed to the lack of emersion during low tides (Young & Kirkman 1975; Poiner 1984) and is known to occur in other creeks, lakes and rivers in south east Queensland where it is referred to as 'river' *Zostera*, in recognition of the larger growth form (C. Conacher, FRC Environmental, pers. comm., J. Phillips, pers. observ.).

Subtidal seagrasses growing along creek banks would be difficult to detect from aerial photographs, particularly from images taken during high tide or during periods of reduced water clarity which would occur on windy days or during turbid periods. Cambridge *et al.* (1974) and WBM Oceanics (2000) used aerial photographs apparently without ground truthing which may explain their failure to observe

FIG. 3. In 1952, extensive sand banks impeded marine flushing of lower Currumbin Creek. A small mangrove community grew on the northern bank of the creek (white arrow). A narrow stream meandered through the sandbanks to the sea (black arrows).

the Currumbin Creek seagrasses. However, Hyland *et al.* (1989) undertook spot dives in Gold Coast estuaries in 1987 and stated that 'seagrass was absent from Currumbin Creek'.

It is unlikely that seagrasses were growing in lower Currumbin Creek when Hyland *et al.* (1989) surveyed the locality in 1987, as between 1974 and 1992 sand dredging was generally removing between 40 000 to 300 000 m³ of sand annually from the internal delta of Currumbin Creek upstream to the Gold Coast Highway bridge (Smith & Jackson 1993; D'Agata & McGrath 2002). Dredging physically destroyed the seagrass habitat and the associated sand destabilisation (Consultancy Study Group 1974; Hollingsworth 1975) would indirectly affect seagrass survival elsewhere in the creek by increasing water column turbidity and/or by burying plants, similar to that reported for other seagrass communities (Larkum & West 1983; Shepherd *et al.* 1989; Morton 1993) for

distances up to 1.2 km from the dredge site (Ellway & Hegerl 1972; Onuf 1994).

Cessation of the sand dredging program probably contributed to the recovery of the Currumbin Creek seagrass community. Different seagrass species vary in the time required to recover from major disturbances which destroy the community (Meehan & West 2000). Recolonisation of *Zostera capricorni* in Botany Bay ravaged by storms which scoured and removed plants took 8 years (Larkum & West 1990), a time period consistent with the development of the large Currumbin *Zostera capricorni* community, assuming seagrass recovery commenced post 1992.

The areal extent of the Currumbin seagrass community in 2003 is far greater than in 1974 when seagrasses were restricted to inside the creek mouth (Consultancy Study Group 1974). Factors responsible for this expansion are not known but changes in salinity, turbidity, degree

of light penetration and human-mediated disturbances affect estuarine seagrass communities. Although *Zostera capricorni* is a euryhaline species and is recorded from habitats experiencing salinities of 3–37 ppt (den Hartog 1970, Harris *et al.* 1980), the species can only tolerate salinities of 2 ppt or less for short periods of time (Kirkman 1975). Prior to 1974, Currumbin Creek was largely a freshwater stream (Consultancy Study Group 1974) and the estuarine section appeared to be confined to near the creek mouth, consistent with the restricted ecological distribution of seagrasses and mangroves to inside the creek mouth.

Changes to the environment and biota of Currumbin Creek over the last 4 decades have not been documented, a similar situation to other Australian east coast estuaries for which historical evidence documenting anthropogenically mediated changes has to be inferred from a variety of sources most notably early maps, air and ground photographs and descriptions (Bird 1974; Recher *et al.* 1993; McLoughlin 2000). Before 1974, Currumbin Creek was predominantly a freshwater stream, with the creek mouth blocked by sand deposition from the longshore transportation and littoral drift until washed away by major rain events (e.g. cyclones) once every 4–5 years (Delft Hydraulics Laboratory 1970, D'Agata & McGrath 2002). This is supported by riparian vegetation in the early 1900s of *Melaleuca* species (paperbarks) typical of brackish/freshwater coastal lagoons in southern Queensland (Dowling & Stephens 2001). After 1974, coastal engineering modifications has kept Currumbin Creek permanently opened to the sea, the marine flushing reducing water turbidity and increasing salinity much further upstream, promoting the observed spread of mangroves and seagrasses to approximately 5 and 2 km upstream respectively. Similar changes to vegetation with increases in salinity have been reported for other east Australian coastal river systems. Bird (1974) reported the loss of *Melaleuca ericifolia*, the invasion of freshwater swamps by saltmarsh vegetation and fluctuations between estuarine *Zostera* and freshwater *Vallisneria* populations were consistent with an increase in salinity in the once freshwater Gippsland Lakes, following the replacement of an intermittent natural opening to the sea with an artificial permanent opening. He also noted that the prolonged build-up of freshwater that preceded the reopening of the natural entrance by flooding is now short lived. The spread of mangroves further upstream in the Brisbane River has also been attributed to the greater penetration of the salt intrusion following dredging of the river mouth (Davie 1990).

Changes in sediment type is also indicative of the shift from freshwater/brackish to a marine conditions in lower Currumbin Creek. Muddy sediments on the northern bank near the creek mouth (Consultancy Study Group 1974; Hollingsworth 1975) are characteristic of sheltered environments which accumulate organic material and silt. Increased water movement from oceanic flushing reworks the sediments and removes organic material and silt and consequently the lower estuary bed is now composed of sand.

This study highlights the urgent need to document the estuarine biota at the species level. These surveys should be undertaken by biologists which the appropriate taxonomic and ecological expertise. Estuaries are dynamic systems, inhabited by species which are spatially and temporally variable in response to fluctuations in environmental parameters. Estuaries are also the sites of intensive human habitation and as such are often impacted by human mediated disturbances. Monitoring for several years is required to collect sufficient data on species composition and abundance in order to distinguish between natural variability and anthropogenically induced impacts on estuaries. Effective environmental management and biodiversity conservation must be based on science and monitoring of species is essential for evaluating whether management strategies are successful in protecting and conserving species. The extensive seagrass community in Currumbin Creek increases habitat heterogeneity for epiphytic algae, juvenile fish and invertebrates, substantially increasing aquatic species richness and as such is a valuable resource that should be not only mapped to adequately document the spatial extent of the community but also monitored and protected.

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